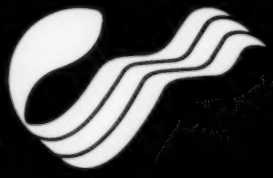

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Optimal Harvest Rate Policies for Rebuilding the Adams River Sockeye Salmon (*Oncorhynchus nerka*)

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Welch, D. W., and D. J. Noakes. 1991. Optimal harvest rate policies for rebuilding the Adams River sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. 48: 526–535.

This paper examines how a currently depressed population, the Adams River sockeye salmon (*Oncorhynchus nerka*), should be rebuilt over time in order to maximize the economic benefit. We use dynamic optimization techniques to answer two questions which previous static optimization work on the Adams River sockeye controversy did not address: (1) what changes from current management policies are required over time to maximize the net economic yield from the population and (2) just how much economic benefit can accrue from following such a policy? We find that following the optimal policy identified by this methodology could contribute more than $600 million to the net value of the Adams River stock. Examination of various confounding factors (comigrating stocks, parameter uncertainty, and the discount rate applied) indicates that the optimal harvest policy is remarkably robust to these sources of uncertainty. The study also lays the basis for repeating such numerical analysis on other populations of interest.

Cet article porte sur la façon de reconstituer progressivement une population qui est présentement réduite, soit le saumon quinnat, (*Oncorhynchus nerka*) de la rivière Adams afin de maximiser les avantages économiques tirés de cette population. Nous appliquons des techniques d'optimisation dynamique à l'examen de deux questions non considérées dans les études d'optimisation statique antérieures qui portaient sur la controverse entourant le quinnat de la rivière Adams : 1) quels changements faut-il graduellement apporter aux présentes politiques de gestion afin de maximiser le rendement économique net tiré de cette population et 2) précisément quels avantages économiques supplémentaires peuvent être tirés de la poursuite d'une telle politique? Nous parvenons à la conclusion que la poursuite de la politique optimale déterminée selon notre méthodologie pourrait équivaloir à plus de 600 millions de dollars en valeur nette du stock de la rivière Adams. L'examen de différents facteurs confusionnels (stocks comigrants, incertitude des paramètres et taux d'escompte appliqué) indique dans tous les cas que la politique de récolte optimale résiste remarquablement à ces sources d'incertitude. En outre, l'étude jette les fondations pour la répétition de telles analyses numériques sur d'autres populations d'intérêt.

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Following the signing of the Canada–U.S. Pacific Salmon Treaty in 1985, responsibility for research on the stocks of sockeye (*Oncorhynchus nerka*) and pink (*O. gorbuscha*) salmon within the Fraser River watershed shifted from the International Pacific Salmon Fisheries Commission (IPSFC) to the Canadian Department of Fisheries and Oceans. Under the terms of this treaty, any additional productivity from salmon populations above historical levels now largely accrues to the country of origin. This agreement provided the incentive for Canada to closely examine the biological data previously collected by the IPSFC over a 40-yr period because the benefits from enhancing the productivity of Fraser River stocks will profit Canada. (Under the terms of the agreement the United States is entitled to some increase in the total catch from the Fraser River, but a cap on the maximum permissible catches means that most of the benefits will flow to Canada.)

Following the release of the data to Canada by the IPSFC, it quickly became apparent that there was significant potential for enhanced production because many sockeye populations within the Fraser River were clearly overexploited (Walters and Staley 1987; Cass 1989). This paper examines how the currently depressed population of sockeye returning to just one tributary of the Fraser River, the Adams River, should be rebuilt in order to obtain the greatest net economic benefit. The Adams River sockeye salmon provides a particularly interesting study illustrating the magnitude of the potential benefit from rebuilding an overexploited population because four nearly independent populations occupy the same spawning and rearing habitat in sequential years, and current escapement levels are far from optimal for three of these populations. Such analysis requires the use of dynamic optimization methods which have not yet been applied to Pacific salmon and which previous static optimization work on the Adams River sockeye controversy (Collie and Walters 1987; Welch and Noakes 1990) did not require.

The reason for the persistence of a cycle in the returns of Adams River sockeye has never been clarified, but in the past managers were reluctant to change this pattern for fear of disrupting the spectacular productivity of the dominant run. Most speculation historically centered about the possibility of an interaction between runs, so that the productivity of weak runs within the 4-yr cycle was suppressed by the dominant run. The early history and good thumbnail sketches of the scientific controversy surrounding this fishery were provided by Ricker (1950) and Ward and Larkin (1964).

Statistical fits of the Ricker stock–recruitment curve to the data for each run were originally thought to support this conjecture because the peak of the curve clearly came at much smaller stock sizes for the three weaker runs. However, fol-

lowing the release of the Adams River data, Walters and Staley (1987) showed that the different productivity levels estimated for each run could reasonably be attributed to a bias in the stock–recruitment analysis caused by cross-correlation between past environmental disturbances and future stock sizes (cf. Walters 1985, 1990). Subsequently, Collie and Walters (1987) examined the statistical fit of Larkin's (1971) stock–recruitment model to the available data, which Larkin had proposed as a model of the potential between-run interaction, and Welch and Noakes (1990) examined the fit of both Larkin's model and a mathematically more tractable model which described the potential between-run interactions using only one parameter (Larkin's model requires three parameters).

Although Collie and Walters' (1987) analysis indicated that some weak interaction might occur, Welch and Noakes (1990) found no statistically significant support for either the Larkin (1971) or generalized model and showed that the residuals for both models were nearly identical to those for the Ricker (1950) model (which, by definition, has no between-run interaction). More importantly, mathematical analysis of the generalized model also showed that the optimal escapement policy for the Adams River stock was to maintain equal escapement in all four cycle years, *even* if between-year biological interactions do occur (Welch and Noakes 1990). Thus, even if significant interaction was obscured by other factors, or if such interaction was to develop following the rebuilding of the runs, there is still an excellent economic rationale for continuing with a rebuilding effort.

Several authors have also looked at various aspects of the potential economic benefits from rebuilding the Adams River population. A priori, it is unclear whether the loss of short-term revenue necessary to allow an accelerated rebuilding schedule can be repaid by higher yields at some later date, as future economic benefits must be discounted to account for the opportunity cost of capital. Evidence that near-term reductions in fishing pressure can increase the total economic value was provided by Walters and Staley (1987), who suggested that an increase in net economic benefits on the order of $150–300 million was possible if fishing pressure on all eight major populations was relaxed in order to let the populations rebuild.

More recent calculations have suggested substantially larger benefits. Collie and Walters (1987) examined the Adams River stock specifically and suggested that yields could be increased on the order of 30–50%. Welch and Noakes (1990) showed that the net present value of having chosen an equal escapement policy for the Adams would have been worth some $3.7 billion more than the IPSFC and present policy of deliberately maintaining the 4-yr cyclical pattern of escapements, assuming that both policies first started from the appropriate escapement optimum.

While there are large differences between these quoted estimates, in part because different studies had different points of departure, the potential value of rebuilding seems clear. However, none of these analyses really addresses the question of obtaining the "optimum optimorum," the very best strategy that can be obtained. Without this information as a guideline, practical difficulties have been encountered in assessing how good are alternative policies that take into account various pragmatic (and principally political) considerations.

In this study, the optimal harvest rate policy is identified using formal optimization procedures, unlike previous studies which have relied more on intuition and trial-and-error simulations. We calculate the optimal stock size trajectory over time for each of the four populations, subject to various biological and economic constraints, whilst taking into account potential losses from comigrating stocks that are harvested along with the Adams River stock. The results of the dynamic optimization work reported here show that the benefits of rebuilding should still be substantial — the Adams River stock alone is worth on the order of $4 billion, with an optimal rebuilding scheme contributing about *$600 million* to this net worth.

The basis for this analysis and the major factors contributing to uncertainty in the analysis are described in the following sections. However, the optimal harvest policy leading to this benefit turns out to be largely unaffected by uncertainty about the exact value of the stock–recruitment parameter estimates or the discount rate used for calculating the value of future economic benefits. The optimal policy also remains unchanged when the comigrating Weaver Creek sockeye and Fraser River pink salmon are included in the analysis. These are the major identified sources of uncertainty in the study.

Stock–Recruitment Analysis

Manipulating the harvest rate applied to the Adams River stock also affects production from comigrating stocks, as these are caught at the same time, and will cause the costs of rebuilding to be underestimated if not accounted for in the analysis. In contrast, biased stock–recruitment (SR) parameter estimates (Walters 1985, 1990) may result in biological productivity (and therefore the benefits of rebuilding) being underestimated.

The timing of the Adams River sockeye migration closely matches the migration of sockeye returning to Weaver Creek, another tributary of the Fraser River, and partially overlaps with the migration of early-run pink salmon to the Fraser River. A transfer-function noise (TFN) model (Noakes et al. 1987) was used to estimate the SR parameters using data from 1948 to 1988 for Adams River and Weaver Creek sockeye and from 1959 to 1987 for Fraser River pink salmon.

A TFN model allows estimation of the SR relationship as well as the correlation structure caused by other factors affecting recruitment. The TFN model was used to estimate the SR parameters because this method permits considerable flexibility in determining the general form of the SR relationship, as well as allowing simultaneous estimation of the autocorrelation structure present in the residuals (Box and Jenkins 1976; Noakes et al. 1987; McLeod and Hipel 1991; but see Walters 1990 for a caveat about the difficulty of correctly estimating the autocorrelation).

Analysis using the TFN model indicates that the sockeye SR data are best described by a Ricker model with a first-order moving average process. The parameters estimated by this method are very similar to those reported by Collie et al. (1990) using a three-stage estimation procedure for the Adams River and Weaver Creek sockeye populations (Table 1). In Collie et al.'s (1990) approach the first-order autocorrelation coefficient is estimated first and then a corrected regression is performed; the TFN method performs the two steps simultaneously. As Collie et al.'s (1990) parameter estimates have also been used in unpublished analyses by working groups within the Department of Fisheries and Oceans, we have adopted these estimates and the uncertainties as documented and reported by Collie et al. (1990) for the Adams River and Weaver Creek sockeye populations but updated the residual variance estimates to reflect more recent data.

Collie et al. (1990) did not report SR parameter estimates for Fraser River pink salmon, so we first attempted to estimate these parameters using the TFN model and data for 1959–87 (Table 1). However, the moving average term estimated by this model was very nearly 1.0, indicating that all the parameter estimates would probably be unstable (Box and Jenkins 1976). We therefore reestimated the parameters of the Ricker model by nonlinear least squares using the simplex algorithm (Mittertreiner and Schnute 1985).

The pink salmon data set includes the 1985 brood year, a year when very cold winter weather is believed to have substantially reduced egg survival (D. Blackbourne, Pacific Biological Station, Nanaimo, B.C. V9R 5K6, pers. comm.). If this data point is excluded from the statistical analysis, the best estimate of the SR function is a straight line (Fig. 1), although the confidence limits on either parameter set are embarrassingly wide. Including the effect of the 1985 brood year in the estimation is therefore conservative because the alternative approach would indicate that there are significant economic benefits to be had from rebuilding the Fraser River pink salmon as well. For this reason, the estimates of the economic benefits from rebuilding reported later use the more conservative values.

Normally, we should correct all of these parameter estimates for a time series bias that causes potential productivity to be underestimated at high stock sizes (cf. Walters 1985, 1990). However, even without correction, very large benefits from rebuilding are predicted and, as we shall show, most of the uncertainty indicates that much greater benefits than we have estimated are possible. We have therefore chosen to be conservative and to conduct our analysis using these parameter estimates without further manipulation.

Mean versus Modal Recruitment Levels

Environmental factors influencing salmon recruitment will likely result in a lognormal recruitment distribution (Peterman 1981). When this is true, the frequency distribution of recruitments will be skewed such that the average recruitment level exceeds the modal, or most probable, level. As the Ricker curve runs thorugh the *modal* recruitment level for each stock size (Hilborn 1985), this raises the interesting question of whether the optimal rebuilding policy should consider the modal, or most likely, recruitment level or the higher value that will be obtained on average over a series of years.

The optimal harvest rate policies reported below are based on the assumption that the modal recruitment level is the best estimate of recruitment strength obtained from a given spawning escapement. Although this tends to underestimate recruitment, the mode is the most probable level of return. A general result is that, although optimal for the most likely level of returns, the calculated policies will tend to overestimate the time required for rebuilding and underestimate both the optimal long-run harvest rate and the average economic benefits from rebuilding.

The chief change to the deterministic policy derived below is that consideration of the effects of stochastic variability should shorten the expected period of painful rebuilding and increase the net present value of the stock dramatically. To first order, average recruitment will exceed modal recruitment by a factor of $e^{\sigma^2/2}$ where σ^2 is the residual variance about the fitted SR curve (Beauchamp and Olson 1973). For the Adams River sockeye, $\sigma^2 = 1.11$ (Table 1), so average recruitment levels will exceed modal levels by a factor of 1.7. Such an increase nearly doubles the economic value of the population and achieves more rapid rebuilding. Maximum economic returns from the fully rebuilt population are therefore attained sooner, and discounted less. If higher than modal recruitment levels occur during the initial rebuilding period, the optimal policy prescription below does not materially change: all returns should be reinvested in the fishery until optimal escapement levels are achieved for each cycle line.

A final point is that the optimal economic harvest rate should climb, *on average*, to near historic levels. To see why this should occur requires calculating the optimal long-run harvest rate. The average recruitment attained at the optimal spawning stock size S^*_{opt} is, for the Ricker curve:

$$(1)\quad R(S^*_{opt}) = S^*_{opt}\, e^{\alpha - \beta S^*_{opt} + \sigma^2/2}$$

where $\sigma^2/2$ is the modal to mean correction factor. The harvest rate required to just maintain the population at this spawning escapement level is defined as

TABLE 1. Comparison of the stock–recruitment parameter estimates obtained using the transfer function noise (TFN) model described by Noakes et al. (1987) with the three-stage regression procedure described by Collie et al. (1990). Parenthetical values for the TFN estimates are the 95% confidence limits; reported values for the Adams River stock are 90% confidence limits and are subjective guesses for the Weaver Creek stock (see Collie et al. (1990) for explanation).

	TFN model[a]				Three-stage procedure[b]			
	α	β	$\theta(1)$	s^2	α	β	$\theta(1)$	s^2
Adams sockeye	2.37 ($\pm$0.27)	4.4×10^{-7} ($\pm 10.8 \times 10^{-7}$)	0.20 ($\pm$0.32)	0.94	2.63 ($\pm$0.14)	6.6×10^{-7} ($\pm 4.4 \times 10^{-7}$)	0.21	1.11
Weaver sockeye	2.41 ($\pm$0.32)	1.4×10^{-5} ($\pm 2.3 \times 10^{-5}$)	0.68 ($\pm$0.24)	0.93	2.63 ($\pm$0.14)	2.3×10^{-5} ($\pm 2.2 \times 10^{-5}$)	0.28	1.37
Fraser pink								
Including 1985 data	2.12 ($\pm$0.70)	2.17×10^{-7} ($\pm 4.14 \times 10^{-7}$)		0.38	—	—	—	—
Excluding 1985 data	1.89 ($\pm$0.80)	1.12×10^{-8} ($\pm 53.2 \times 10^{-8}$)		0.35	—	—	—	—

[a]Because an analytic estimate of the Ricker α parameter is not available when using the TFN model, the stated estimate was calculated by nonlinear least squares using the simplex algorithm (Mittertreiner and Schnute 1985), with the β parameter constrained to the TFN estimate.
[b]The Ricker α estimate is an aggregate value estimated for the 10 Fraser River stock reported in Collie et al. (1990).

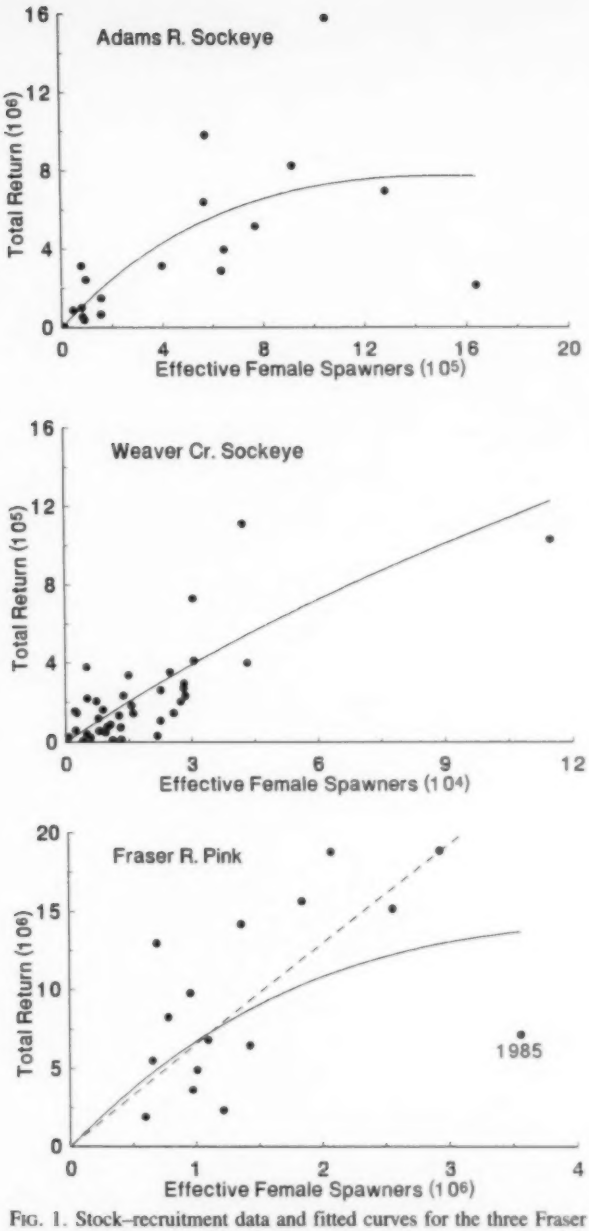

FIG. 1. Stock–recruitment data and fitted curves for the three Fraser River populations considered. The stock–recruitment curve for pink salmon obtained by excluding the 1985 observation (broken line) is also shown.

$$(2)\quad h^*_{opt} = \frac{\text{Recruits} - \text{Escapement}}{\text{Recruits}}$$

or

$$(3)\quad = 1 - \frac{\zeta S^*_{opt}}{R(S^*_{opt})}$$

$$(4)\quad = 1 - \frac{\zeta\, e^{-\sigma^2/2}}{e^{\alpha - \beta S^*_{opt}}}.$$

(The factor ζ is required to convert the number of successful female spawners to the equivalent number of recruits.)

Using the parameters appropriate for Adams River sockeye (Table 1), and the estimated optimal escapement level of $S^*_{opt} = 1.1 \times 10^6$ effective females, the deterministic estimate ($\sigma^2 = 0$) of the optimal long-run harvest rate is $h^*_{opt} = 0.74$. The *stochastic* estimate using $\sigma^2 = 1.11$ leads to $h^*_{opt} = 0.85$, a level similar to, or perhaps even slightly greater than, historic harvest levels (see below).

The difference between these two estimates is important, but not cause for concern. The long-run harvest rate calculation is appropriate for populations already at the optimal escapement level, but it does not describe the harvest rates that yield the maximum net economic benefit when the population must first be moved to the optimum. Past escapement levels for the Adams River sockeye were far from optimum. The calculated long-run harvest rate is also the rate necessary to maintain the population at the optimum *on average*. In the absence of a reliable forecast of returning run strength, in any given year the best initial estimate of the harvest rate is the deterministic estimate. This rate should only be increased once the optimal escapement target has been assured.

Numerical Analysis

The Model

Establishing the optimal harvest policy involves identifying those harvest rates that maximize the net present value of the population (catch in dollars, with future returns discounted). A numerical model was used to examine the effect of different harvest rate policies on the late-migrating component of the Fraser River sockeye and pink stocks. Optimal policies were found by calculating the harvest parameters for each cycle line that maximize the net present value (NPV) of the fishery over a 100-yr time horizon.

Most studies of optimal harvesting strategies for fisheries management have relied on some variant of dynamic programming to find the optimal policy (cf. Walters and Hilborn 1976; Parma 1990). A serious practical difficulty with dynamic programming is that, although conceptually elegant, computational demands grow explosively as more realistic models are developed to satisfy managers' concerns that the model captures all the important features of the fishery.

An important tactical aspect of this study is our approach of estimating the optimal harvest rates directly, by numerically maximizing the NPV of the model with respect to the harvest rate parameters. This avoids some of the computational difficulties usually associated with optimization by dynamic programming. We used the simplex algorithm for the parameter estimation (Mittertreiner and Schnute 1985). Using this approach allows successively more realistic models to be examined without the rapid growth in computational demands that are normally experienced. The model incorporated multiple stocks, differential maturation rates, and stock-specific SR parameter estimates. (The remaining parameters required in the analysis, apart from the SR estimates, are given in Table 2.) Optimization started using the escapement estimates for the four brood years 1986–89 to forecast modal recruitment strengths for 1990 onwards.

The prices at which sockeye and pink salmon are valued (Table 2) are important when comparing the trade-off of one species against another during rebuilding, or for evaluating the economic loss involved in choosing a suboptimal policy. These prices were suggested as estimates of wholesale value-added

TABLE 2. Additional parameters used in the rebuilding analysis. ζ is the estimate of the inverse of the sex ratio and is needed for correcting from stock in units of "effective females" to estimates of stock as total recruitment.

Stock	Price ($·fish^{-1})	Maturity		ζ[a]
		Age 4	Age 5	
Adams sockeye	20	0.995	0.005	1.74
Weaver sockeye	20	0.911	0.099	1.85
Fraser pink	2	—[b]	—[b]	1.70

[a]Inverse of the sex ratio, corrected for partial spawning success.
[b]All pink salmon mature at age 2.

prices (R. Mylchreest, Department of Fisheries and Oceans, 555 West Hastings St., Vancouver, B.C. V6B 5G3, pers. comm.). They probably underestimate the value of the fish to Canada in our opinion, and their use will therefore undervalue the loss involved in adopting suboptimal policies. Their use as *relative* indicators of the value to Canada of sockeye and pink salmon is more reasonable.

The effect of discounting is to reduce the relative value of future catches, and the choice of an appropriate discount rate is somewhat arbitrary. We define the NPV of the catch under a given harvest rate policy as the total value over time, with future catches discounted at a rate of $\delta = 4\%$ per annum, because harvesting costs are fixed and largely independent of any single stock. Historically, the real rate of return on investment (i.e. returns corrected for inflation) has averaged about 4–5%. In contrast, Walters (1986) suggested that even lower discount rates may be appropriate when valuing the future returns from common property resources, while the Treasury Board of Canada has mandated that the benefits from projects supported by the public purse should be evaluated using a discount rate of 10% per annum.

Using a discount rate of $\delta = 4\%$, the value of a given number of fish is halved in 17 yr and reduced to less than 2% by the end of 100 yr. All simulations were run to a time horizon of 100 yr, although the effect of the 4% discount rate ensures that events happening much more than 25 yr in the future have little economic impact on the results. The effect of the discount rate is examined below, but the optimal policy turns out to be essentially invariant under a wide range of assumptions about the appropriate discount rate.

Harvest rates for each cycle line were defined using a four-parameter sigmoid curve of the form

$$(5)\quad h(t) = h_1 + h_2\frac{(1-h_1)t}{t+e^{a-bt}}.$$

This curve defines an initial harvest rate of h_1 at $t = 0$ which then asymptotically approaches an invariant long-run harvest rate of $h^*_{opt} = h_1 + h_2 - h_1h_2$. The two parameters a and b define the rate at which the harvest rate function changes between the initial and final harvest rates and, depending on sign, also allows the long-run optimum harvest rate to be approached from either above or below. This formulation also permits the harvest rate to be constrained so that in any year it must be a value of $h_1 = h_{min}$ or greater.

A total of 16 parameters (four per cycle line) must be estimated. During initial work, several other harvest rate parameterizations were examined, but to ensure sufficient control over the constrained analyses described below, a total of four parameters per cycle line were always required. The most general formulation used a set of independent and unconstrained harvest rate parameters for each of the first 16 yr, with the last four parameters describing the fixed harvest rate applied thereafter to each cycle line. In all cases, the harvest rate manipulations required to obtain the maximum yield were always completed by the sixteenth year.

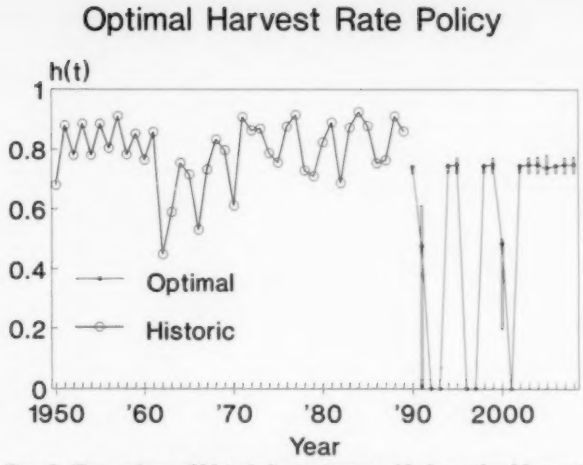

FIG. 2. Comparison of historic harvest rates with the optimal harvest policy. Vertical bars indicate 95% confidence limits on the harvest rate estimates.

Despite the flexibility possible by having 16 free harvest rate parameters, we always found that the optimization based on the four sigmoid harvest rate functions resulted in net yields equal to or very slightly greater than those obtained using 16 independent parameters. The results we report here are therefore those obtained using equation (5); as the results show, even a step-function response is possible using this formulation.

Results

Single-Stock Optimal Policy

The years 1990–93 correspond to the return of the dominant, subdominant, and two off-year runs to the Adams River. The optimal harvest rate policy for the Adams River sockeye alone (Fig. 2) shows that the policy maximizing NPV is to reduce harvest rates on the dominant run by about 10% to achieve the estimated optimum harvest rate, $h^*_{opt} = 0.74$, and to reduce the harvest rate on the subdominant run the following year to 50%. The optimal policy for the off-year runs is to close the fishery and prevent all harvesting until these runs rebuild.

Under this policy the dominant and subdominant runs rebuild to the escapement level producing maximum yields in one cycle, while the off-cycle years take approximately three cycles (12 yr). Harvesting of the subdominant run at the long-run optimum therefore begins in 1995.

As the Ricker parameters are inversely related to potential yield (high α or low β values both leading to higher yields), the extrema of the 95% confidence intervals (i.e. $\alpha \pm CI_\alpha$; $\beta \pm CI_\beta$) can be used to calculate the uncertainty in the optimal harvest rate trajectory caused by uncertainty in the SR parameters. The results (vertical bars in Fig. 2) show that the optimal harvest rate policy identified is rather insensitive to uncertainty in the SR parameter estimates. Optimal long-run harvest rates vary by only a few percent from the maximum

likelihood estimates (a value much smaller than historic fluctuations in the harvest rate), and the time to rebuild under these alternative SR scenarios (Fig. 3) remains essentially unchanged.

The greatest uncertainty involves the appropriate optimal harvest rate for the subdominant Adams River run in 1991, but even under quite optimistic assumptions about productivity, harvest rates well below historic levels are indicated. As the confidence intervals on the recruitment projections are indicated, most of the uncertainty about the magnitude of the rebuilt recruitment levels is already on the upper limit; recruitment levels much larger than the rebuilding projections also lie within the confidence limits.

Impact of Mixed-Stock Harvesting

Returning Adams River sockeye comigrate with sockeye returning to the Weaver Creek spawning grounds, and the tail end of these runs return during the start of the pink salmon migration to the Fraser River. The harvest rate chosen for managing the Adams River stock will therefore also apply equally to the Weaver Creek stock and will also partially affect the Fraser River pink run.

Stock–recruitment data for the Weaver Creek population show little evidence that further increases in stock size would substantially increase recruitment levels, and the abundance of the four cycle lines are already at rough parity (Cass 1989). Harvest rates optimal for the Adams River will therefore lead to overescapement to the Weaver Creek stock. Both loss of immediate catch (particularly in the weak off-cycle years) and subsequent depression of future recruitment levels by overescapement will decrease the potential benefits from rebuilding the Adams River stock. In contrast, even a conservative analysis of the available SR information for Fraser River pink salmon indicates that some rebuilding of these stocks might also be appropriate.

The greatest difference in harvest rates from the optimal single stock harvest rate policy is less than 1% in any given year, assuming a 100% overlap in either the migration timings of the Adams River and Weaver Creek sockeye stocks alone or the two sockeye stocks plus the Fraser River pink salmon together. Optimal population trajectories for the two-stock case are illustrated in Fig. 4. The inclusion of Weaver Creek sockeye has little effect on the optimal policy because the potential benefit from rebuilding the off-year Adams River stock is much larger than the near-term losses from the Weaver Creek stock.

A more detailed examination of the catch and escapement trajectories for the two stocks shows that the imposition of a harvest moratorium during the off years imposes large population fluctuations on the Weaver Creek stock (Fig. 5). These initially occur because of the reduced harvest rates, but they also continue for several cycles after the Adams River stock is rebuilt because of continued overescapement.

The effect of including the Fraser River pink salmon in the optimization is similar to that of including the Weaver Creek sockeye because, although numerically abundant, pink salmon are only worth one tenth as much as sockeye. As the estimated harvest rates make clear, despite the initial loss of catch from other stocks and some subsequent suppression of recruitment due to overescapement, the net benefits from rebuilding the Adams River run are not seriously affected by considering other comigrating stocks.

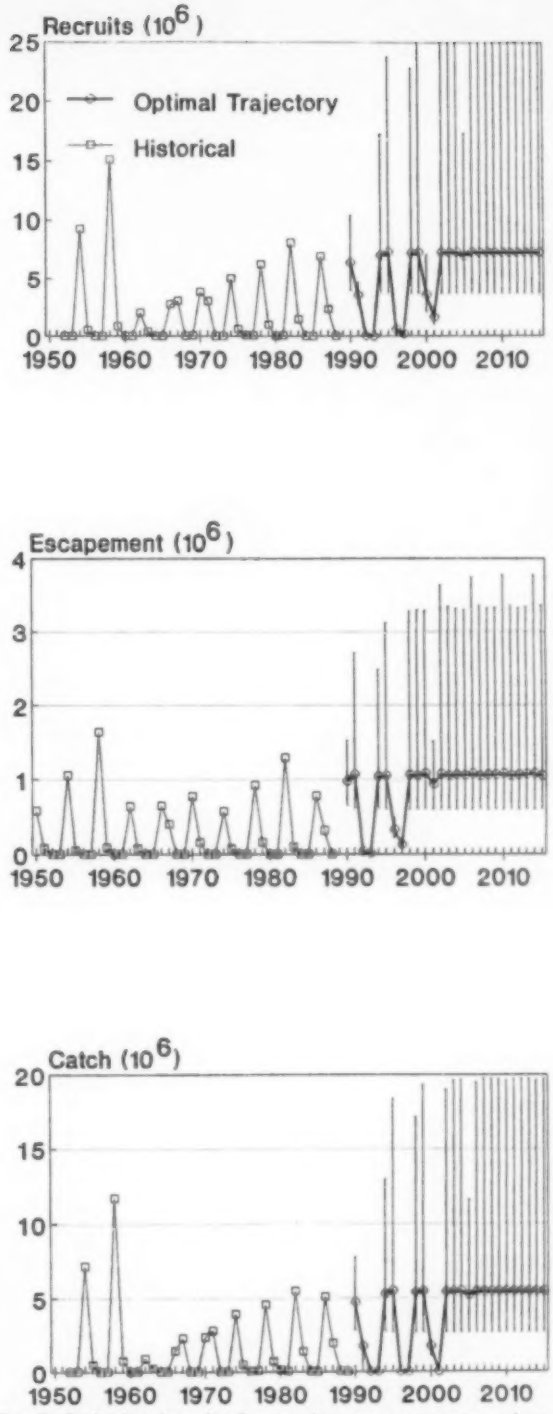

FIG. 3. Optimal trajectories for recruitment, escapement, and catch for the Adams River sockeye. The cyclic pattern in the historic data is clearly evident.

Effect of Imposing a Harvest Rate Floor

Although consideration of comigrating stocks does not seriously alter the optimal harvest rate policy, a complete fishing

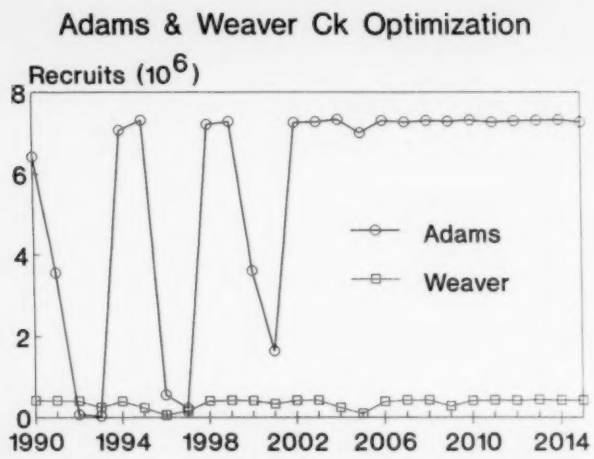

FIG. 4. Recruitment trajectories for the two-stock optimization. Note that predicted recruitment to the two off-cycle Adams River runs equals or exceeds mean recruitment levels to Weaver Creek by the second cycle.

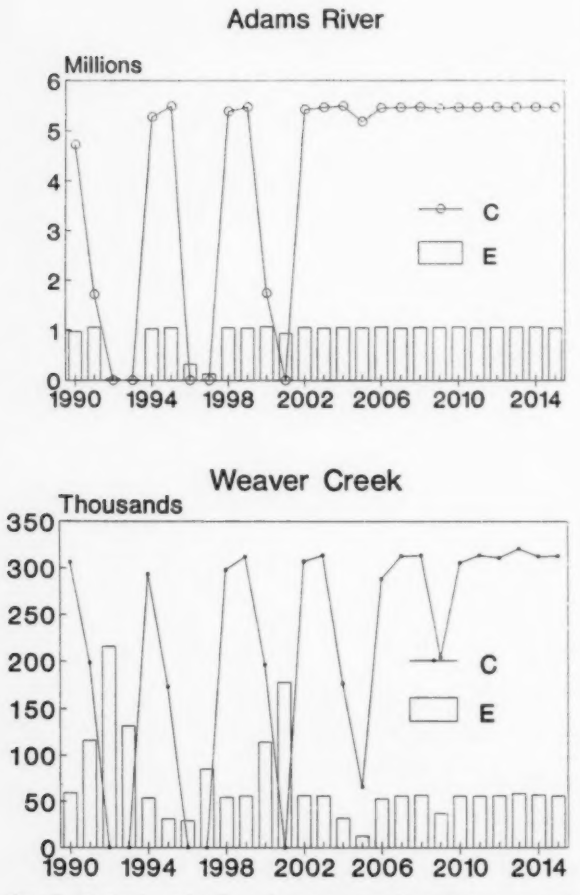

FIG. 5. Optimal catch (C) and escapement (E) trajectories for the Adams River and Weaver Creek stocks. Note the difference in scales for the two graphs.

moratorium during migration of the off-year Adams River stocks is a break with past practice unlikely to be viewed with enthusiasm by many elements of the fishing community. Choosing such a management strategy would involve the expenditure of considerable political capital, further reduce the limited credibility of scientists involved in the management process, and could introduce severe distortions into the fishery if fishing times are maintained within historical limits.

Such practical concerns have motivated much of the emphasis on incremental rather than radical changes to current fishing plans. But how much would be lost if less severe harvest rate restrictions were imposed? An aboriginal food fishery within the Fraser River, guaranteed under treaty provisions, imposes about a 5% harvest rate on Fraser River stocks (FRSTF 1988). In addition, American fishermen are entitled to Fraser River sockeye under the terms of the Canada–U.S. treaty (although not necessarily to catches from specific stocks), and fisheries geographically removed from the Fraser River also catch Adams River sockeye. In general, harvest rates lower than 50% are difficult to achieve for any Fraser River run whilst maintaining historic fishing patterns (K. McGivney, Department of Fisheries and Oceans, Planning Branch, 555 West Hastings St., Vancouver, B.C. V6B 5G3, pers. comm.).

To examine the effect of choosing a suboptimal policy where harvest rates do not decline in the short term to their optimal levels, we constrained the feasible harvest rate policies by requiring initial harvest rates to lie at or above some minimum. To be specific, we examined the loss in NPV entailed by stipulating some minimum value below which harvest rates must never fall (harvest minima greater than this level are allowed, if optimal). This is obtained by specifying a value for h_1 in equation (1) for those cycle lines where optimal harvest policies would otherwise drop below this minimum. The remaining parameters are then optimized subject to the constraints.

As the minimum permissible floor on harvest rates is increased, the NPV of a rebuilt Adams River stock declines relatively smoothly (Fig. 6). For each 10% increase in the minimum harvest rate the NPV initially declines by about $25 million for either the deterministic or stochastic harvest rate calculation. Under the stochastic recruitment assumption the constrained harvest rate trajectories are similar to the deterministic calculation shown in the top panel, but approach the long-run stochastic average of $h^*_{opt} = 0.84$. Specifying a harvest rate floor of 50% constitutes a minimum net loss of $121 million in yield relative to the optimal policy.

There is some question as to whether even a reduction to a 50% harvest rate for the two off-cycle years would be acceptable, as roughly 10 million pink salmon return to the Fraser River in odd years. Neither fishermen nor managers are likely to support a rebuilding program that would mean a significant reduction in the length of the pink salmon fishing season without good expectation of very significant future returns.

To quantify the potential losses from choosing a suboptimal strategy, four alternative policies were examined (Table 3). For the first ("Optimistic") policy, managers were canvassed for their opinion as to what were the lowest harvest rate floors currently thought acceptable by senior management. In this scenario, harvest rates for the two weakest years are reduced to 50%, but harvest rates for the dominant and subdominant runs are only lowered to the long-run optimal level. In the second ("Pessimistic") policy, a 50% floor on harvest rates is permitted only for the first of the two weak years, when no pink salmon return to the Fraser. The third ("Long-Run") policy is

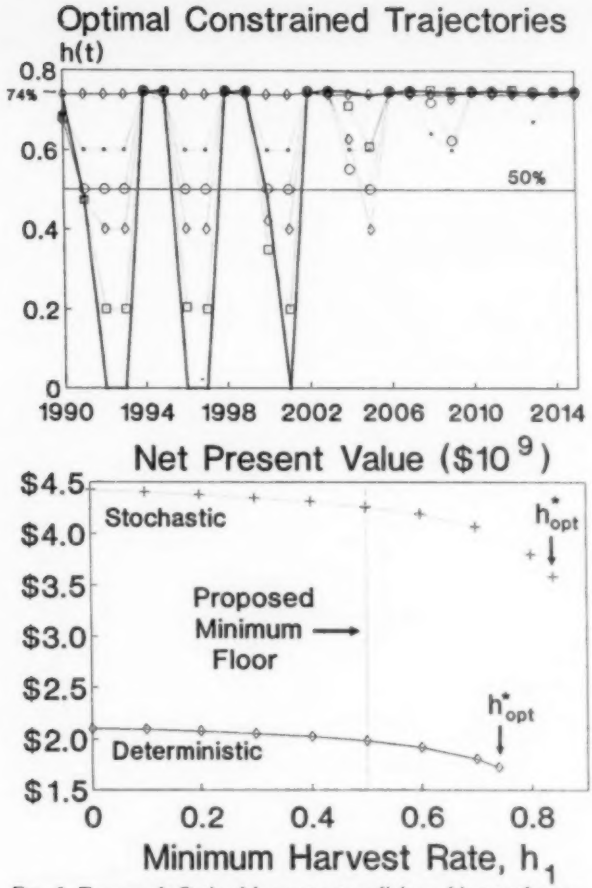

FIG. 6. Top panel: Optimal harvest rate policies subject to the constraint that rates must not drop below 0, 20, 40, 50, 60, and 74% for the deterministic model. Bottom panel: Decline in the net present value of the Adams River stock resulting from a specified floor on harvest rates. Values under both the deterministic and stochastic recruitment assumptions are shown.

TABLE 3. Calculated losses for four alternative management policies relative to the optimal policy for the Adams River stock. (The optimal policy would increase the net present value of the Adams River stock to about $2.1 billion and $4.4 billion under the deterministic and stochastic recruitment assumptions.) Harvest rates for the four cycle years are shown in parentheses for each policy; boldface figures indicate imposed harvest rate floors that are above the optimal level, but below the long-run optimum.

	Loss (millions of dollars)	
Policy	Deterministic	Stochastic
1. Optimistic (0.74, 0.74, **0.5, 0.5**)	143	175
2. Pessimistic (0.74, 0.74, **0.5**, 0.74)	261	314
3. Long-run optimum (0.74, 0.74, 0.74, 0.74)	382	440
4. Status quo (0.8, 0.8, 0.8, 0.8)	676	630

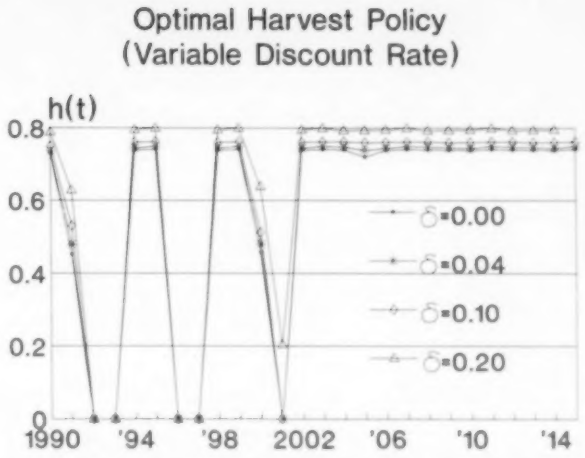

FIG. 7. Optimal harvest rate policies (calculated for the Adams River stock only) assuming annual discount rates of 0, 4, 10, and 20% per annum.

to reduce, and maintain, all harvest rates at the long-run optimum of 74%, but to allow no further harvest rate reductions to speed up the rebuilding process. The fourth ("status quo") policy is to do nothing and persist with the current harvest rates of 80%. For the stochastic calculations, the harvest rate floors of 74% are replaced by 80%.

Relative to the optimal policy, the economic losses under these strategies could range up to a billion dollars, especially as very conservative assumptions have been used in estimating the SR parameters (Table 3). The potential benefits of adhering closely to the optimal harvesting strategy are clearly great and therefore worth considering carefully.

Influence of the Discount Rate on the Optimal Policy

All of the analysis reported to this point indicates that the optimal harvest rate management policy for the Adams River stock over the next decade is quite different from that previously in force. However, this assumes that a 4% per annum discount rate is reasonable. Higher discounting of future catches is appropriate when perceived levels of risk are higher or passing on the resource to future generations is considered less important. Conversely, if the preservation and enhancement of the resource for future times is considered more important, a lower discount rate may be appropriate.

The influence of the discount rate on the optimal harvest rate policy and population trajectories is minor for a wide range of assumed discount rates (Fig. 7). Regardless of the discount rate chosen, the optimal strategy always involves a harvest rate moratorium on the off-year runs for at least two cycles. If the *extremely high* real rate of return of $\delta = 0.20 \cdot yr^{-1}$ is assumed (perhaps appropriate if fishermen with very high mortgage rates and little confidence in the success of rebuilding do the economic valuation), optimal long-run harvest rates are only slightly greater than is the case for more realistic discount rates. Even in this case, fishing of the off-years should only start during the third rebuilding cycle. Thus, again, the optimal harvesting strategy is insensitive to the specific assumptions used.

Discussion

To briefly recap, the optimal harvest rate policy for rebuilding the Adams River sockeye is to fish the subdominant run at

a 50% harvest rate in 1991 and to impose a moratorium on fishing the off-year runs for two to three cycles (8–12 yr). In essence, the optimal policy reinvests all gains from a reduced harvest rate into further increases in spawning stock biomass until the optimal escapement level is attained. At that point, harvesting is reinitiated. This is the same result previously found by other workers who examined simpler optimal harvesting problems (Walters and Hilborn 1976; Conrad and Clark 1987; Parma 1990).

This policy remains invariant when uncertainty about the SR parameters is considered, remains essentially independent of the economic discount rate assumed, and does not change when the presence of comigrating stocks is factored into the analysis. The predicted economic losses associated with choosing some suboptimal alternative policy are surprisingly large (especially to those used to the rather informal decisions made under the rubric of "expert judgement"). They obviously need to be carefully considered before settling on a final management policy.

The current analysis points out several important aspects of the general rebuilding process for the Adams River sockeye. First, the potential for rebuilding weak runs to the Adams River greatly exceeds the potential loss of catch from the Weaver Creek and Adams River sockeye. This had previously been raised as a serious impediment to rebuilding during discussions within the Department of Fisheries and Oceans. Simply put, the value and the dynamics of the Adams River sockeye relative to the other populations determine both the broad details and the finer aspects of the optimal rebuilding process.

That the economically optimal policy should remain so invariant to the sources of uncertainty discussed is a reflection of the enormous potential gains from rebuilding the Adams River sockeye. It should also be noted that we have erred on the side of conservatism wherever possible, particularly by not attempting to correct for bias in the SR estimates. Plausible sources of bias may lead to significantly underestimating the benefits of rebuilding (Walters 1985, 1990).

There are, nevertheless, factors which have not been considered. Chief among these, closure of the Adams River fishery during the off-cycle years will reduce fishing times and therefore affect employment within the fishery. This, or any other marked change from past fishing practice, is likely to prove a sensitive issue.

As presently formulated, the optimal harvest rate policy is therefore optimal, but not very practical. Its chief use is to identify the best policy in a world where there are no serious impediments to its implementation and therefore to show just how much economic loss may be associated with choosing other management strategies that would be less controversial.

The losses associated with these alternative strategies are sobering and were clearly not recognized during earlier meetings of experts charged with developing an experimental rebuilding plan for the Adams River sockeye. At those meetings, discussion centered on how to extract the greatest scientific information from a small set of preselected rebuilding strategies (those numbered 2–4 in Table 3). A criticism of these discussions (briefly described by Collie et al. 1990) was that it was impossible to assess the potential losses associated with these intuitive strategies because no one knew what the optimal strategy was and therefore how much loss was entailed in choosing a different strategy.

Having calculated the "optimum optimorum," it is clear that very significant losses may be associated with these alternate proposals — perhaps a billion dollars (Table 3). Further, the statistical power of even the most aggressive of the alternative rebuilding proposals described in Table 3 means that there would be about a one in three chance of drawing the wrong conclusion about whether mechanisms hampering rebuilding really do exist, even after 8 yr (Collie et al. 1990), and the economic losses could be on the order of $200 million.

For the rebuilding plan currently thought most likely to be accepted by senior management (a reduction of the harvest rate to 50% for the first off-year alone), these potential losses jump to roughly $100 million, while the power of the experiment was calculated to be about 58%! Put in perspective, the probability of making the correct conclusion at the end of 8 yr would be little greater than could be achieved by simply tossing a fair coin at the outset. By this time, much of the economic gains from rebuilding will, in any event, have been lost because of the need for discounting. (An advantage of the coin tossing experiment is that the expected value of this "experiment" would be $200 million — the probability of immediately following an aggressive rebuilding strategy, multiplied by the expected yield.)

That formal optimization methods can yield such startling improvements over proposals developed intuitively by experts is neither new nor surprising (cf. Tversky and Kahneman 1974; Slovic et al. 1977; Dawes 1979; Boutillier et al. 1988). It does clearly suggest that equally impressive gains from the application of rigorous optimization methods to other fisheries problems may be possible. The challenge is to have these approaches accepted by those involved in the day-to-day management of the fisheries.

Acknowledgements

We thank Dr. Jeremy Collie, University of Alaska, for a particularly useful review.

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Changes in Abundance of Two Percids, *Perca fluviatilis* and *Gymnocephalus cernuus*, along a Productivity Gradient: Relations to Feeding Strategies and Competitive Abilities

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Bergman, E. 1991. Changes in abundance of two percids, *Perca fluviatilis* and *Gymnocephalus cernuus*, along a productivity gradient: relations to feeding strategies and competitive abilities. Can. J. Fish. Aquat. Sci. 48: 536–545.

Relative abundances of perch (*Perca fluviatilis*) and ruffe (*Gymnocephalus cernuus*) were studied in eight lakes ranked along a gradient of increasing productivity. The diets of perch and ruffe in relation to food resources were quantified over a 5-mo period in one lake of moderate and one lake of high productivity. The abundance of perch decreased and that of ruffe increased along the productivity gradient. Large perch ate fish over the whole season in the more productive lake, but rarely ate fish in May and June in the less productive lake. All size classes of ruffe fed mainly on macrobenthos in both lakes. The diversity of macrobenthos was higher in the lake of low productivity, as was the diet breadth of ruffe. The abundance patterns of perch and ruffe are likely related to the simultaneous effect of increasing prey abundance and decreasing light penetration with increasing productivity. Furthermore, the abundance of perch is likely affected by increasing interspecific competition and that of ruffe by decreasing predation pressure as productivity increases.

L'abondance relative de la perche d'Eurasie (*Perca fluviatilis*) et de la grémille (*Gymnocephalus cernuus*) a été étudiée dans huit lacs classés par ordre croissant de productivité. Le régime alimentaire de ces espèces a été mesuré en fonction des ressources alimentaires, sur 5 mo, dans un lac peu productif et dans un lac très productif. Plus le gradient de productivité était élevé, moins la perche était abondante et plus la grémille l'était. La perche de grande taille se nourrissait de poisson tout au long de la saison dans le lac le plus productif, mais s'en nourrissait rarement en mai et en juin dans le lac le moins productif. Dans les deux lacs, la grémille de toutes les classes de taille se nourrissait principalement de macrobenthos. Le macrobenthos du lac le moins productif était plus diversifié que l'autre, ce qui se reflétait dans le régime alimentaire de la grémille. Il existe probablement des rapports entre les régimes d'abondance de la perche et de la grémille et l'effet simultané de l'abondance croissante des proies et de la moindre pénétration de la lumière à mesure que s'accroît la productivité. En outre, l'abondance de la perche doit probablement être influencée par la concurrence interspécifique accrue et celle de la grémille, par la diminution de la pression de prédation à mesure que la productivité augmente.

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Generally, when European lakes are ranked from low to high productivity, a pattern of species succession in the fish community is observed. The typical pattern is as follows. At low productivity salmonids are abundant, at higher productivity percids first increase and then decrease in abundance, and at high productivity cyprinids are very abundant (Leach et al. 1977; Hartmann and Nümann 1977; Leopold et al. 1986). Two common Eurasian percids, perch (*Perca fluviatilis*) and ruffe (*Gymnocephalus cernuus*), follow this general pattern, but the decrease for ruffe occurs at higher productivities than for perch (Leach et al. 1977). The decrease in perch abundance in lakes of high productivity has been related to competition with roach (*Rutilus rutilus*) for zooplankton (Persson 1983, 1986; Persson and Greenberg 1990). In addition, Bergman (1990) found evidence that perch were affected by the presence of ruffe and suggested that perch and ruffe might compete for benthic macroinvertebrates. Also in a field experiment, ruffe affected the growth of perch (E. Bergman and L. Greenberg, unpubl.).

Perch and ruffe have different feeding strategies, as ruffe rely on both visual and nonvisual sensory organs, while perch is a visual hunter. The foraging ability of ruffe is less influenced by light than that of perch (Bergman 1988). These results correspond well with the different abundances of perch and ruffe in lakes of different productivities (i.e. turbidity) (see also Bergman 1990). Thus, increased competition between perch and roach and possibly ruffe in combination with lower light levels in lakes of high productivity are two factors that could explain the different responses of perch and ruffe to increased lake productivity.

Besides competition, predation is a factor that can influence population regulation. However, it is only recently that shifts in the importance of competition and predation as structuring factors on different trophic levels along an environmental gradient (productivity) have been discussed (e.g. Oksanen et al. 1981; Persson et al. 1988). In the model presented by Persson et al. (1988), predation is viewed as a more important regulating factor for the fish communities in lakes of moderate productivity whereas competition is more important in lakes of high productivity. Differences between young perch and ruffe in susceptibility to predation could therefore be a third factor influencing the abundances of the two species.

TABLE 1. Chlorophyll *a*, transparency, area, and maximum depth for eight Swedish lakes in July or August. The area value from Lakes South and North Osby includes both basins, and the data from Lake Sövde are from late September. Data were obtained from Hamrin (1973) (Lakes South and North Bolmen), Hamrin et al. (1974) (Lake Ivö), Gelin and Ripl (1978) (Lake Hinna), Collvin and Persson (1975) (Lakes South and North Osby), Gelin (1971) and Hamrin (1984) (Lake Vomb), and unpublished data (Lake Sövde).

	Chl *a* (μg/L)	Secchi depth (m)	Area (km^2)	Max. depth (m)
Lake South Bolmen	2–4	5.0	41.2	37.0
Lake Ivösjön	2–4	5.0	54.2	50.0
Lake North Bolmen	5	3.0	7.6	13.0
Lake Hinnasjön	4	2.2	0.3	2.5
Lake South Osbysjön	9	1.8	Σ5.2	2.5
Lake North Osbysjön	13	1.0	Σ5.2	5.0
Lake Vomb	62	0.75	12.8	16.0
Lake Sövdesjön	66	0.7	2.8	8.0

The purpose of this study was to examine the differences in distribution of perch and ruffe. The study included a comparison of eight lakes of different productivity. Two of these lakes, one of moderate productivity and one of high productivity, were studied in more detail to discern seasonal patterns in diet and habitat use of perch and ruffe. The distribution patterns of the two species within and between lakes were related to the species' competitive abilities under different light and temperature conditions and to interactions with cyprinid species.

Materials and Methods

Lake Description

Sampling was conducted at eight locations of varying productivity in six South Swedish lakes. The localities (hereafter lakes) were ranked by productivity (chlorophyll *a*) in July–September (Table 1). The two lakes that were studied in more detail were Lakes South Bolmen and Vomb. Lake South Bolmen is a medium productive lake with submersed vegetation and some reed vegetation. The bottom consists of sand and mineral matter at water depths up to approximately 5 m and orgnic matter in deeper areas. Lake South Bolmen is rather deep (maximum depth 37 m, mean depth 8 m) and is usually thermally stratified during at least part of the summer. Lake Vomb is a highly productive lake (Table 1), almost lacking submersed vegetation but with some reeds. Regulation of the water level limits the area of emergent vegetation. In the shallower parts of the lake, i.e. to depths of ~3–4 m, the bottom consists of sand and at deeper depths consists of organic matter. Lake Vomb (maximum depth 16 m, mean depth 6 m) is exposed to winds and is seldom thermally stratified.

Field Sampling

Data on fish abundances were obtained from my investigations of Lake Sövde (1982), Lake South Bolmen (1985), and Lake Vomb (1986) and from previous studies of Lake South Bolmen (Hamrin 1973), Lake Ivö (Hamrin et al. 1974), Lake North Bolmen (Hamrin 1973), Lake Hinna (Gelin and Ripl 1978), Lake South Osby (Collvin and Persson 1975), and Lake North Osby (Collvin and Persson 1975). Sampling was performed with 1.5-m-deep survey link gill nets of a length of 56 m. Eight mesh sizes (9, 14.5, 18, 25, 30, 33, 38, and 46 mm) each 7 m long were used. At each locality, gill nets were set on the bottom at several depths for 1–3 d during May, July, or August in different years. All fishing data are presented as catch per unit effort (CPUE) which is catch per net for 24 h in either numbers or biomass.

Five additional samplings in Lake South Bolmen (May–October 1985) and Lake Vomb (May–September 1986) included fish, zooplankton, benthic invertebrates, dissolved oxygen concentration (Winkler method), light transmission, and temperature. To sample the fish, I used survey link gill nets of the same type as described above that were placed on the bottom at six depths (2, 5, 10, 15, 20, and 25 m) in Lake South Bolmen and four depths (3, 6, 9, and 12 m) in Lake Vomb. In Lake South Bolmen, each sampling lasted for three 24-h periods and in Lake Vomb only for one 24-h period because of the higher total abundance of fish in Lake Vomb. Captured fish were identified, measured (total length), weighed, and counted. In addition, stomachs from perch and ruffe were removed and deep-frozen for later diet analysis. Perch and ruffe were divided into several size classes (approximately year classes) and, if possible, 10 stomachs from each size class at each depth were taken. Due to the low numbers of stomachs in each size class, size classes sometimes had to be combined into wider classes. Size classes of ruffe differ between lakes due to the different size distributions in the two lakes. Zooplankton samples were taken at each fish sampling location with a 2-m-long plastic core placed as close as possible to the bottom. Ten- and 5-L samples were taken from Lake South Bolmen and Lake Vomb, respectively. Samples were sieved through a 45-μm filter and the zooplankton were preserved in 4% formaldehyde. The benthic invertebrates were sampled at every second depth that had been sampled for fish (5, 15, and 25 m) in Lake South Bolmen and at every depth that had been fished in Lake Vomb. Six samples were taken at each locality using an Ekman grab (area 225 cm^2). The material was sieved through a 0.5 mm net and deep-frozen for later analysis.

Laboratory Analyses

The zooplankton and the benthic invertebrates were identified, counted, and measured (length). Length measurements of zooplankton were used to convert abundance to biomass using length–weight regressions given in Bottrell et al. (1975). For benthic macroinvertebrates, length–weight regressions from a south Swedish pond (Persson and Greenberg 1990) and from Smock (1980) were used. The diversity of the benthic macroinvertebrate community was expressed by using the Shannon–Wiener index ($-\Sigma\ P_i \cdot \ln\ P_i$ where P_i is the proportion of organism i in the sample).

Stomach contents of perch and ruffe were identified, counted, and measured. Dry weights of items eaten were estimated using length–weight regressions as described above. Due to small sample sizes in some size classes, statistical analyses could not always be performed. Diet breadths for perch and ruffe were calculated using Levins' (1968) niche breadth measure:

$$B = \frac{1}{\Sigma\ |P_i \cdot P_i|}$$

where P_i is the proportion of food item i in the diet.

Results

Chemical and Physical Data

Lake South Bolmen was thermally stratified during June, July, and August but not in May and October. Surface

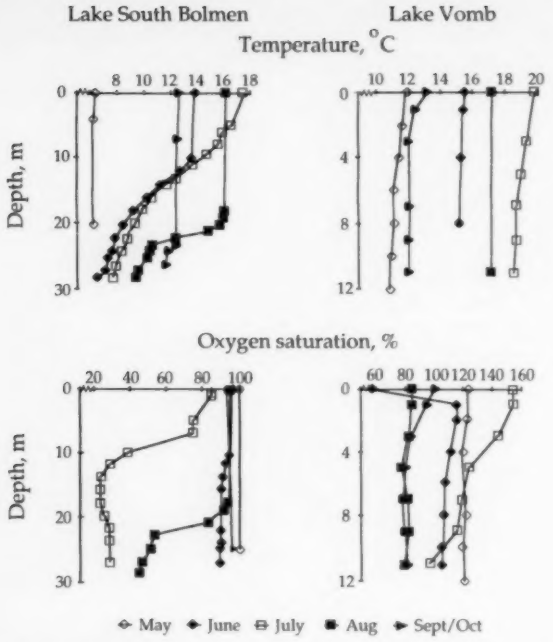

FIG. 1. Temperature and oxygen concentrations at different depths during May, June, July, August, and September/October in Lake South Bolmen and Lake Vomb.

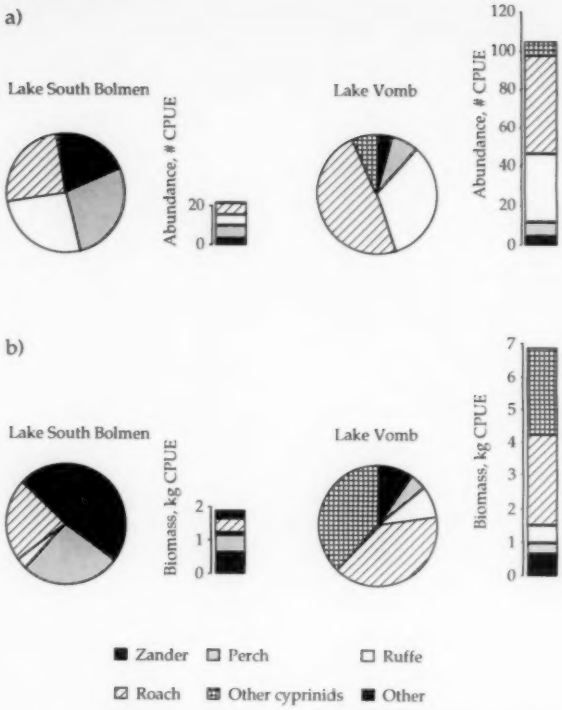

FIG. 2. Composition of the fish community in Lake South Bolmen (1985) and Lake Vomb (1986). Calculations are based on CPUE. Circles shows relative composition and the bars show means for the whole season (=5 mo). (a) Based on numbers of fish; (b) based on weight of fish.

temperature varied between 6 and 18°C and bottom temperature between 6 and 12°C (Fig. 1). Lake Vomb was never thermally stratified (May–October) and the surface temperature varied between 11 and 20°C. The largest difference between surface and bottom temperature was 1.5°. Dissolved oxygen concentrations were high at all sampling dates in Lake Vomb, and during the summer there was a strong supersaturation due to high phytoplankton production. In Lake South Bolmen, dissolved oxygen was high at all sampling dates except in the hypolimnion in July (23%) and August (40%) (Fig. 1). Water transparency varied between 3.6 and 5.0 m in Lake South Bolmen and between 0.2 and 1.0 m in Lake Vomb (Table 2).

Fish Community

The total CPUE was more than five times higher in Lake Vomb than in Lake South Bolmen (Fig. 2a). In Lake South Bolmen the fish fauna was dominated by percids (28% perch, 26% ruffe, and 6% zander (*Stizostedion lucioperca*)), which together made up 60% of the total number of captured fish. Cyprinids, such as roach, formed only about 25% of the total captured. In Lake Vomb, 55% of the total number of fish were cyprinids (48% roach and 0.3% bream (*Abramis brama*)). Ruffe were the most common percid and constituted 33% of the total number of captured fish. The proportion of perch and zander was 7 and 5%, respectively. Approximately the same pattern was present when biomass was substituted for numbers. The main difference was that ruffe, which constituted a large number of the total abundance, only constituted a small part of the total biomass. In contrast, bream composed a small number of the total abundance but a large part of the total biomass

TABLE 2. Secchi depth, depth at 10% of surface light level, and temperature in Lake South Bolmen (1985) and Lake Vomb (1986).

	Secchi depth (m)		10% light (m)		Temperature (°C)	
	Bolmen	Vomb	Bolmen	Vomb	Bolmen	Vomb
May	5.0	0.8–1.0[a]	2.4	2.1	6.1	11.8
June	4.2	0.3–0.5[a]	2.4	1.1	13.8	15.5
July	3.6	0.2–0.4[a]	2.5	0.9	17.5	19.8
August	3.6	0.4	2.2	1.5	16.1	17.2
September	—	0.7	—	1.3	—	13.2
October	4.0	—	2.6	—	12.6	—

[a]Estimated from light transmission curves.

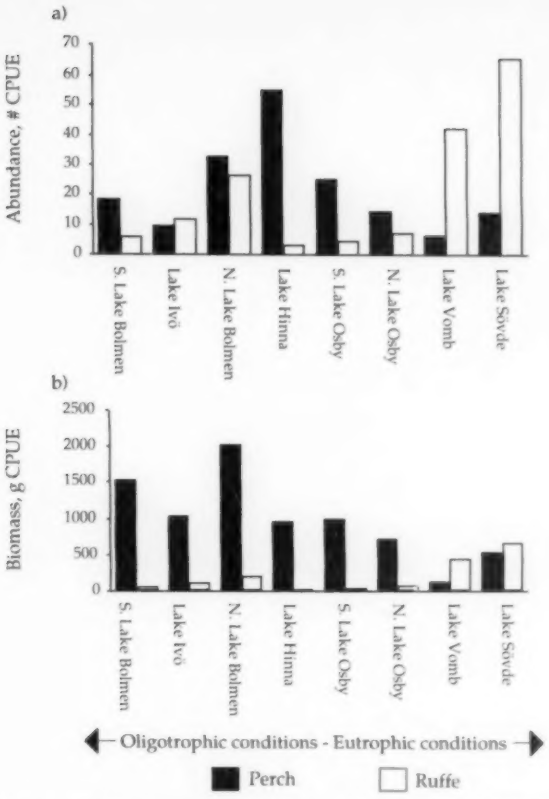

FIG. 3. (a) Abundance and (b) biomass of perch and ruffe in eight South Swedish lakes ranked along a gradient of increasing chlorophyll *a* values. CPUE is based on numbers or grams of fish. The data are obtained from one fishing occasion during the summer season.

(Fig. 2b). The category "other" includes burbot (*Lota lota*), vendace (*Coregonus albula*), whitefishes (*Coregonus lavaretus* and *C. oxyrhynchus*), and a few northern pike (*Esox lucius*). This group formed 24% of the total biomass and 15% of the total abundance in Lake South Bolmen.

The numerical abundance (CPUE) of perch first increased and then decreased when the lakes were ranked from low to high productivity. The biomass abundance (CPUE) of perch decreased continuously over the productivity gradient ($r^2 = 0.48$, $P < 0.05$). The different patterns obtained for perch from numbers and biomass were a result of a decrease in mean size of perch along the productivity gradient (see also Persson 1983). In contrast, the CPUE (numbers and biomass) of ruffe increased with increasing productivity ($r^2 = 0.76$, $P < 0.01$ for numbers and $r^2 = 0.83$, $P < 0.01$ for biomass) (Fig. 3). The low abundance of ruffe in Lakes Hinna, North Osby, and South Osby might be related to the shallowness of these lakes.

The length distribution of both perch and ruffe differed between Lake South Bolmen and Lake Vomb (Fig. 4). Ruffe were bigger in Lake Vomb than in Lake South Bolmen whereas the opposite was the case for perch (chi-square $P < 0.001$ for both perch and ruffe).

Vertical Distribution of Perch and Ruffe

Perch were more abundant in shallower than in deeper water in both Lake South Bolmen and in July and October in Lake Vomb (Fig. 5). Ruffe were rather evenly distributed between all depths in both lakes, although fewer ruffe were caught at 9 m than at other depths in Lake Vomb. In Lake South Bolmen there was no seasonal difference in the vertical distribution of perch (chi-square $P = 0.24$), but there was a higher abundance of ruffe at shallower depths in May compared with July and October (chi-square $P < 0.03$) (Fig. 5). Catches, however, were higher in May than in July and October; if relative abundance is considered, this difference is not clear. In Lake Vomb,

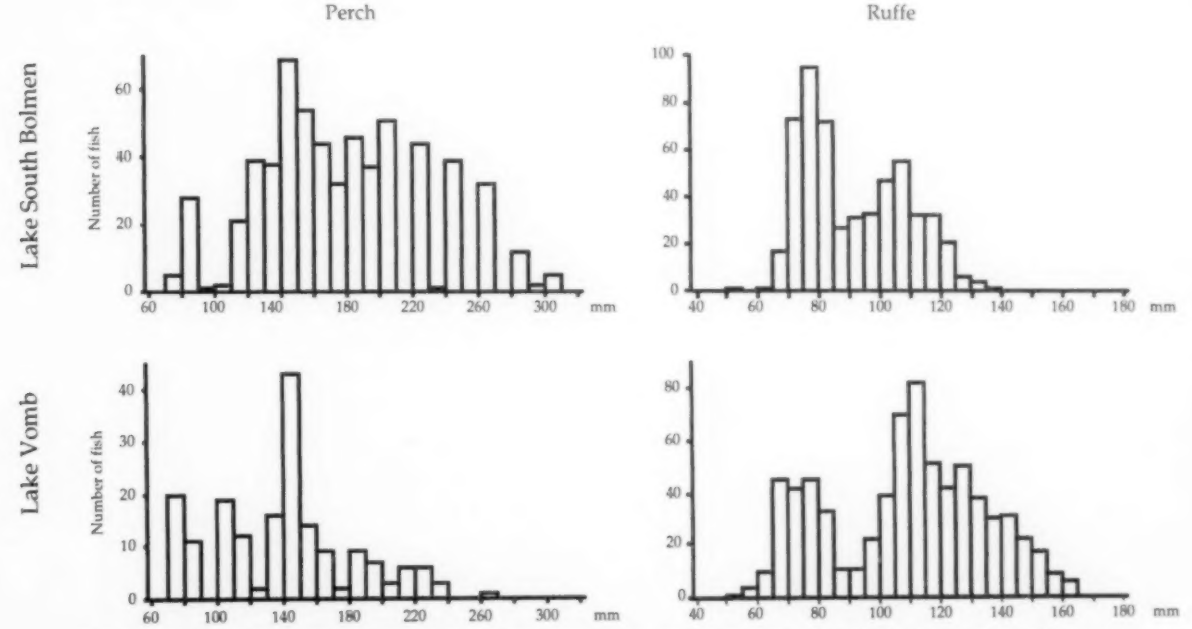

FIG. 4. Length distribution of perch and ruffe in Lake South Bolmen and Lake Vomb. Note the different scales on the *y*-axis.

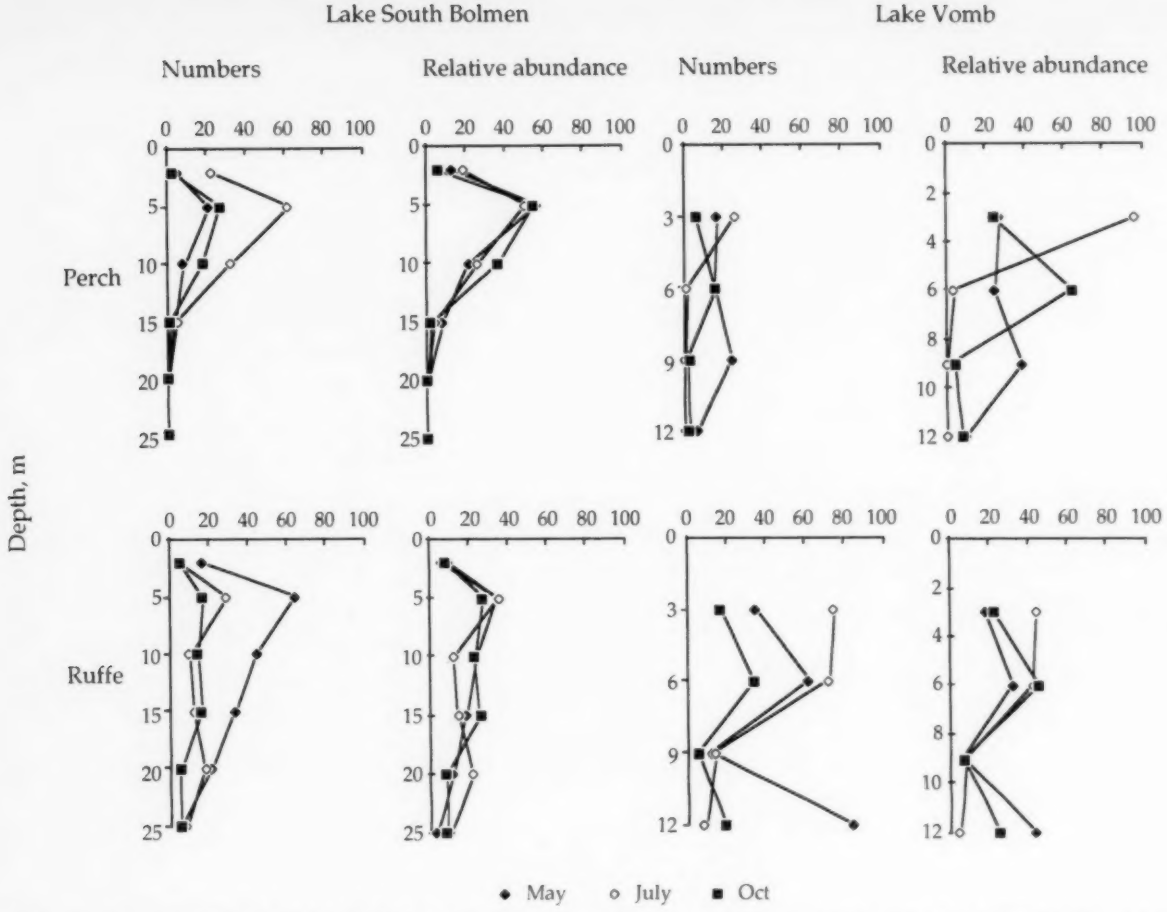

FIG. 5. Vertical distributions of perch and ruffe in Lake South Bolmen and Lake Vomb during May, July, and October. The distributions are presented both as numbers and relative abundance.

perch were more restricted to the shallowest depth in July than in May and September (chi-square $P < 0.001$). Ruffe were less abundant at the deepest depth in July and October in Lake Vomb (chi-square $P < 0.001$) (Fig. 5); looking at the relative abundance, this is the case for July only.

To compare differences between years, complimentary analyses were run for Lake South Bolmen on data from July and October 1970, 1971, 1972, and 1985. The thermocline was most developed in July 1970, almost absent in 1971, and intermediate in 1972 and 1985. There was a difference between the vertical distribution of perch in July and October in 1970, but not in the other years (chi-square $P < 0.001$ in 1970, $P = 0.13$–0.60 in 1971, 1972, and 1985). For ruffe there was generally not a difference between the vertical distribution in July and October (chi-square $P = 0.051$ in 1970, $P = 0.072$ in 1971, $P = 0.38$ in 1972, and $P = 0.080$ in 1985). There was a large between-year variation in both perch and ruffe abundance (chi-square $P < 0.001$ for both July and October).

Prey Resources

Total biomass of copepods was about five times higher in Lake Vomb than in Lake South Bolmen on all sampling dates (Fig. 6). In May and June, the biomass of cladocerans was higher in Lake Bolmen than in Lake Vomb. The opposite was true in August and September–October when the biomass in Lake Vomb was about 10 times that in Lake South Bolmen (Fig. 6). There was no depth effect on biomass of cladocerans or copepods in the two lakes (ANOVA $F_{1,4} = 0.62$–1.96, $P = 0.12$–0.61). In Lake South Bolmen there was a minimum in cladoceran biomass in July (repeated measures ANOVA $F_{1,4} = 11.95$, $P < 0.001$), but not in copepod biomass (repeated measures ANOVA $F_{1,4} = 2.09$, $P = 0.12$). In Lake Vomb there was an increase in cladoceran biomass over time (repeated measures ANOVA $F_{1,4} = 28.12$, $P < 0.001$). For copepods the time effect was more variable, with the lowest biomass in May and the highest in June (repeated measures ANOVA $F_{1,4} = 3.53$, $P = 0.040$).

The total biomass of benthic macroinvertebrates was similar in Lake Vomb and Lake South Bolmen in July but two to four times higher in Lake Vomb than in Lake South Bolmen in the other months (Fig. 7). The diversity of the benthic macroinvertebrate community was higher in Lake South Bolmen than in Lake Vomb (t-test $t = 5.3$–19.9, $P = 0.003$–0.0001). There was no relationship between depth and diversity except in June in Lake Vomb when the diversity increased with increasing depth ($F_{1,2} = 34.91$, $P < 0.03$). The dominant benthic

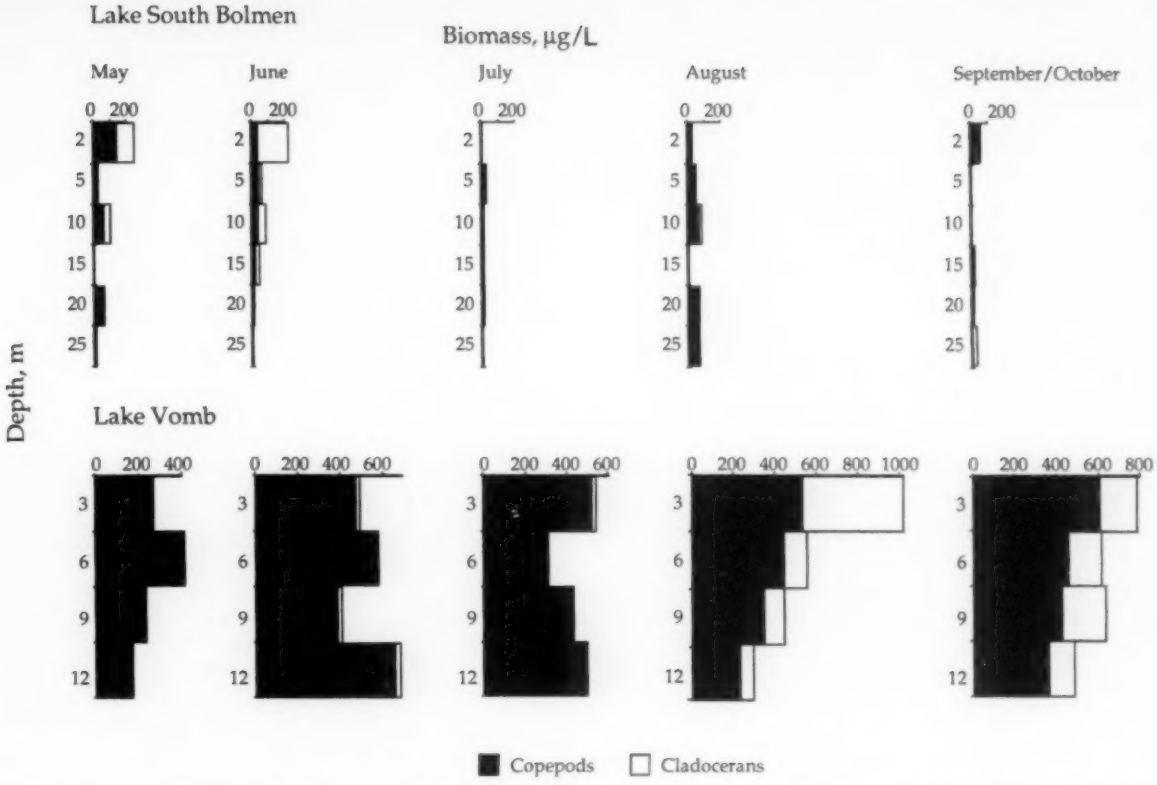

FIG. 6. Total biomass of copepods and cladocerans at different depths during May, June, July, August, and September/October in Lake South Bolmen and Lake Vomb.

macroinvertebrates in Lake South Bolmen were chironomids, ephemeropterans, and *Pisidium* (Fig. 7). There was a decrease in biomass of chironomids, ephemeropterans, and *Pisidium* with increasing depth (Table 3). The dominant benthic macroinvertebrates in Lake Vomb were chironomids, with *Pisidium* constituting a smaller fraction (Fig. 7). There was a minimum in chironomid biomass in July. At the same time, chironomid biomass decreased in July and increased in August with increasing depth (Table 4).

There was no difference between the lakes in the proportion of biomass of macrobenthos to cladocerans (*t*-test $P = 0.80$) whereas the ratio of macrobenthos to copepods was significantly lower in Lake Vomb than in Lake South Bolmen (*t*-test $P < 0.001$).

Diets

In Lake South Bolmen, the diets of the two smallest size classes of perch were dominated by zooplankton and macroinvertebrates (ephemeropterans) whereas the diet of the largest size class was dominated by fish and macroinvertebrates (*Sialis* and ephemeropterans). In Lake Vomb, the two smallest size classes mainly fed on zooplankton and macroinvertebrates (chironomids) and the diet of the largest size class was dominated by fish (Fig. 8). The main differences between the two lakes were that small perch included more macroinvertebrates in their diet in Lake Vomb than in Lake South Bolmen and that the largest perch included more macroinvertebrates in Lake South Bolmen than in Lake Vomb (Fig. 8). Although no small or medium perch were caught in Lake Vomb in July and August and the sample size of the middle class from Lake Vomb was small, the data indicate that only the largest size class fed on fish. In contrast, the middle size class perch in Lake South Bolmen included fish in their diet (Fig. 8). The largest size class of perch in Lake South Bolmen ate more fish than the smaller size classes during June, July, and August (ANOVA $F_{2,14-47} = 11.6–43.07$, $P = 0.002–0.0001$). A similar pattern was present in Lake Vomb in May and September (the sample sizes of the other months were too small to make comparisons possible) (ANOVA $F_{2,9-27} = 10.22–34.50$, $P = 0.001–0.0001$).

The diets of ruffe were dominated by benthic macroinvertebrates in both lakes, although some zooplankton was eaten (Fig. 9). In Lake South Bolmen the diet of ruffe was diverse and the prey items were chironomids, ephemeropterans, trichopterans, *Sialis*, *Asellus*, *Pisidium*, copepods, and cladocerans. In Lake Vomb the diet of ruffe was less diverse and was dominated by chironomids (76–90%), with some *Pallasea*, *Pisidium*, cladocerans (e.g. *Diaphanosoma*), and copepods. In July, ruffe also consumed a small amount of fish in both lakes. The higher prey diversity in the diet of ruffe in Lake South Bolmen compared with Lake Vomb complements the higher diversity of macroinvertebrate preys in Lake South Bolmen.

There were no major diet differences between size classes of ruffe, except in August in Lake South Bolmen where the largest ruffe ate more copepods than the smallest size class (ANOVA $F_{2,74} = 5.29$, $P < 0.01$) (Fig. 9). The diet breadth of ruffe

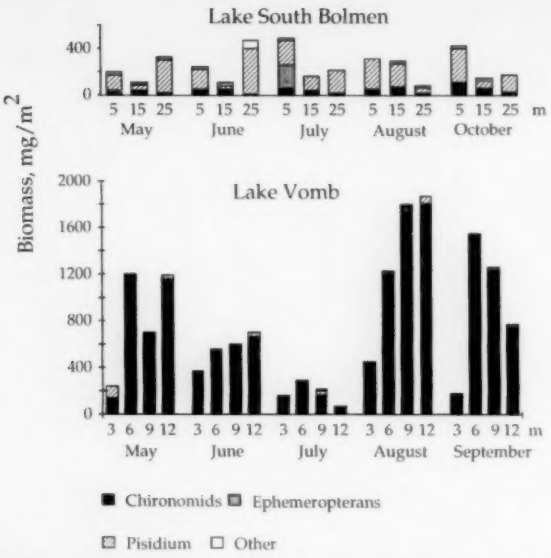

FIG. 7. Total biomass of chironomids, ephemeropterans, *Pisidium*, and other invertebrates at different depths during May, June, July, August, and September/October in Lake South Bolmen and Lake Vomb.

TABLE 3. Repeated measure ANOVA testing the effect of time (season), depth, and time × depth on the biomass (log transformed) of chironomids, ephemeropterans, *Pisidium*, and total gastropods in Lake South Bolmen.

	df	*S*	*M*	*F*	*P*
log chironomids					
Time	4	5.598	1.400	1.34	0.27
Depth	2	56.793	28.397	20.26	0.0001
Time × depth	8	9.323	1.165	1.12	0.37
log ephemeropterans					
Time	3	6.150	2.050	1.22	0.31
Depth	2	29.806	14.903	9.24	0.002
Time × depth	6	12.301	2.050	1.22	0.31
log *Pisidium*					
Time	4	12.622	3.156	1.66	0.17
Depth	2	28.111	14.055	4.65	0.027
Time × depth	8	58.938	7.367	3.88	0.001
log total gastropods					
Time	2	0.050	0.025	0.020	0.98
Depth	2	2.115	1.058	0.98	0.40
Time × depth	4	5.169	1.292	1.01	0.42

was larger in Lake South Bolmen than in Lake Vomb over the whole season (*t*-test $t_{90-195} = 2.56–5.62$, $P = 0.01–0.0001$) whereas no general pattern was found for perch.

Discussion

The abundance of perch in my study decreased in the more productive lakes. This is in accordance with the results of Leach et al. (1977) who found that perch first increased and then decreased in abundance along a gradient from low to high productivity. The general pattern of a decrease in the abundance

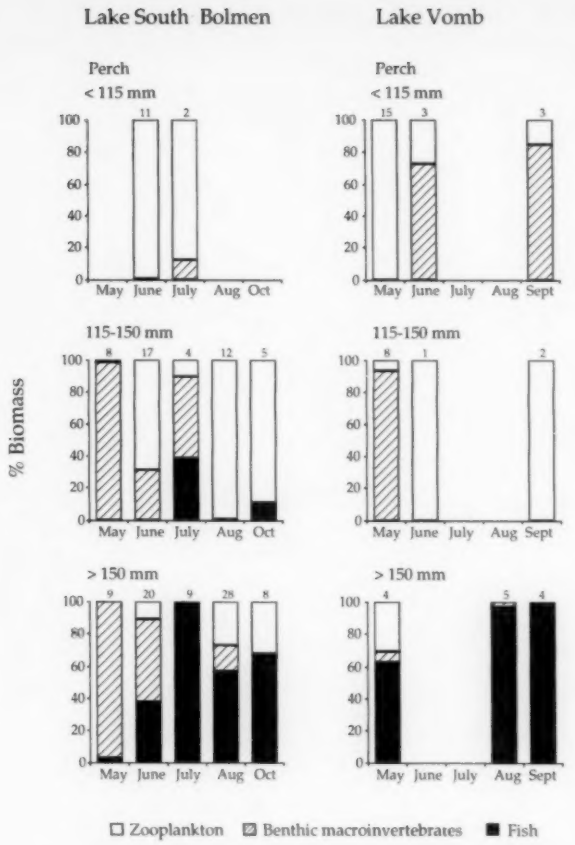

FIG. 8. Diet of different size classes of perch during May, June, July, August, and September/October in Lake South Bolmen and Lake Vomb. Food groups are fish, benthic macroinvertebrates, and zooplankton. The numbers above each bar represent the sample size.

TABLE 4. Repeated measure ANOVA testing the effect of time (season), depth, and time × depth on the biomass (log transformed) of chironomids and *Pisidium* in Lake Vomb. The analysis for ephemeropterans and gastropods was not done because of too small sample sizes.

	df	*S*	*M*	*F*	*P*
log chironomids					
Time	4	44.665	11.166	12.44	0.0001
Depth	3	22.481	7.494	5.75	0.007
Time × depth	12	32.148	2.679	2.98	0.002
log *Pisidium*					
Time	3	7.212	2.404	1.19	0.32
Depth	3	20.886	6.692	4.56	0.016
Time × depth	9	35.493	3.944	1.96	0.064

of perch in very low productive lakes (Biró 1977; Entz 1977; Hartmann and Nümann 1977; Kitchell et al. 1977) is not present in my data, perhaps because no lakes had such low productivity. The abundance of ruffe was low in the lakes of moderate productivity and increased in the lakes of high productivity. Leach et al. (1977) reported that ruffe decreased in

abundance at a somewhat higher productivity than perch, not apparent in this study. Still, my results are in general correspondence with the results of previous studies (Biró 1977; Entz 1977; Hartmann and Nümann 1977; Kitchell et al. 1977; Leach et al. 1977). However, these studies do not provide any mechanisms for the observed patterns. It is for example only recently that the decrease of perch in lakes with higher productivity has been related to competition with roach for zooplankton as a consequence of roach's higher foraging capacity on zooplankton (Johansson 1987; Johansson and Persson 1986; Persson 1983; Persson 1987a, 1987b). Hayward and Margraf (1987) suggested food limitation as an underlying mechanism for the decreased growth of yellow perch (*Perca flavescens*) in the parts of Lake Erie with highest productivity. Much less is known, however, about the competitive relationships between ruffe and other species.

An earler study (Bergman 1988) has shown that the foraging ability of perch depends more on light than does that of ruffe (see also Disler and Smirnov 1977). As increased productivity results in increased algae turbidity and hence decreased light penetration (Leach et al. 1977), perch may have a competitive disadvantage in highly productive lakes compared with ruffe. This could partly explain the differences in abundance between perch and ruffe in lakes of varying productivity. Perch foraging ability is also more affected by temperature than that of ruffe (Bergman 1987, 1988). Perch showed a strong avoidance of deeper depths in July compared with May and October in Lake Vomb and in Lake South Bolmen the year when the lake had a strong thermocline. This seasonal variation in vertical distribution of perch in Lake South Bolmen and Lake Vomb indicates that effects of both light and temperature influence the vertical distribution of perch. In contrast, ruffe are present at all depths in all seasons. Thus, fewer habitats are available for perch than for ruffe, which may decrease the competitive ability of perch relative to that of ruffe.

As expected, fish and prey biomass were positively correlated with each other, with fish and prey biomass being greater in Lake Vomb than in Lake South Bolmen. Differences in fish species composition between the two lakes are more difficult to explain based solely on the food resources. However, the lower light penetration in Lake Vomb probably affects prey availability, more for perch than for ruffe becasue perch's foraging ability is more sensitive to changes in light (Bergman 1988). The relatively higher abundance of perch in Lake South Bolmen than in Lake Vomb could also be affected by seasonal changes in cladoceran biomass. In Lake South Bolmen the highest biomass of cladocerans was in May and June whereas in Lake Vomb the biomass was low until August and September. Consequently, young-of-the-year perch in Lake Vomb probably experience a food shortage early in life when they are presumably more sensitive to starvation. The macroinvertebrate biomass in Lake South Bolmen did not show any seasonal pattern whereas in Lake Vomb it was much lower in July. Competition may be higher during the summer in Lake Vomb, which is in accordance with conclusions of other studies (Andrusak and Northcote 1971; Nilsson 1960; Persson 1983, 1987a; Persson and Greenberg 1990; Zaret and Rand 1971; Werner and Hall 1977). The fish abundance pattern in Lake Vomb, with relatively few perch but large numbers of roach and ruffe, is in accordance with Bergman (1990) who showed that the growth of perch, but not ruffe, was affected by competition with roach (i.e. roach density).

Perch undergo substantial ontogenetic niche shifts. First they

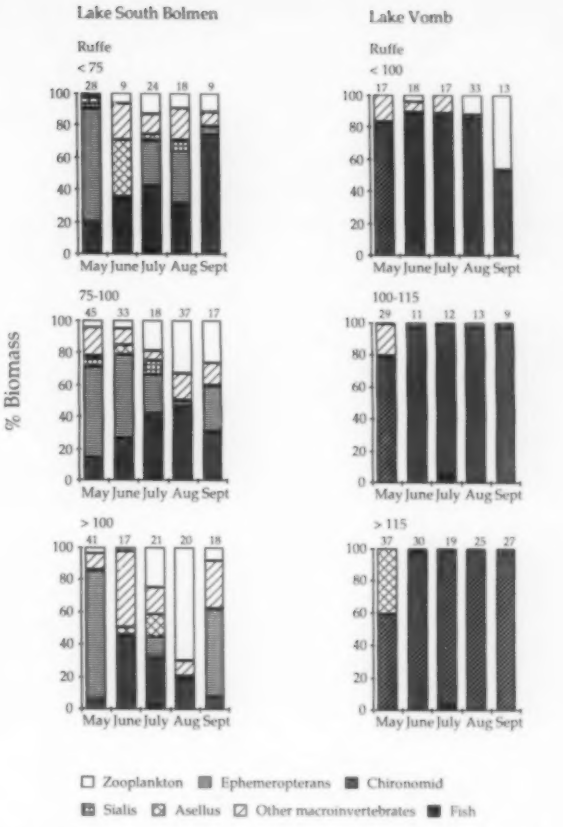

FIG. 9. Diet of different size classes of ruffe during May, June, July, August, and September/October in Lake South Bolmen and Lake Vomb. Food groups are fish, ephemeropterans, chironomids, *Sialis*, *Asellus*, other macroinvertebrates, and zooplankton. The numbers above each bar represent the sample size.

feed on zooplankton, then on benthic macroinvertebrates, and finally on fish (Collette et al. 1977; Hartmann and Nümann 1977; Persson 1988), which was also the case in this study. The only difference between perch in the two lakes was that large perch in Lake Vomb ate a higher proportion of fish during the whole season whereas in Lake South Bolmen, perch ate a lot of fish only during the summer months. Ruffe do not grow as large as perch, and they do not show the same degree of diet shift with an increase in size as perch (Collette et al. 1977; Hartmann and Nümann 1977). This is indicated by the relatively similar diet of the different size classes of ruffe. The correspondence between a high diet niche breadth of ruffe and high diversity of benthic macroinvertebrates in Lake South Bolman compared with the situation in Lake Vomb also indicates that ruffe is a food generalist (see also Densen 1985).

A high abundance of roach forces perch to shift from feeding on zooplankton to benthic macroinvertebrates at an earlier stage than if the abundance of roach is low (Persson 1986; Persson and Greenberg 1990). As a benthivore, ruffe (Aleksandrova 1972; Densen 1985; Johnsen 1965) is not expected to compete with planktivorous roach to any larger extent, and ruffe is thus not expected to decrease with increasing productivity. A field experiment (Bergman 1990) supports the idea that ruffe growth

is unaffected by roach density. It is not known whether ruffe is a more efficient feeder on benthic macroinvertebrates than perch. However, the high abundance of ruffe in lakes of high productivity might affect perch negatively, as ruffe may compete with macrobenthos-feeding perch under conditions of poor light conditions and high turbidity (see also Bergman 1990).

Ruffe are heavily preyed upon by zander (Biró 1973), which may influence the abundance of ruffe in lakes of low productivity. Adult perch cannibalize their juveniles and zander also eat perch (Alm 1946, 1952; Hartmann and Nümann 1977; Holcík 1977). However, zander and perch are active during different periods, thus reducing predation by zander on perch (Ali et al. 1977). Similar patterns have been reported for walleye (*Stizostedion vitreum vitreum*) and yellow perch (Kelso and Ward 1977). Apparently, predation pressure on ruffe is higher than that on perch. A recent hypothesis has suggested that there is a shift from predation to competition as the main factor structuring fish communities along the productivity gradient (Persson et al. 1988; see also Oksanen et al. 1981). The lower abundance of ruffe in lakes in low productivity could thus also be a result of high predation in those lakes.

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Development and Stability of Fish Assemblages after Lime Treatment

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Appelberg, M., and E. Degerman. 1991. Development and stability of fish assemblages after lime treatment. Can. J. Fish. Aquat. Sci. 48: 546–554.

Long-term effects of limestone treatment on fish populations in acidified lakes in Sweden have been examined since 1983 to assess the development and stability of fish assemblages after lime treatment. In total, 77 lakes were sampled twice using standardized methods between 1983 and 1988. The lakes were limed 1–16 yr before the second sampling. Physical and chemical variables and the fish data were reduced using PCA ordination and the resulting relationships were analyzed using linear regression and ANOVA. Relationships between the fish assemblage characteristics and the environmental factors were highly dependent on the species composition of the assemblages. The number and diversity of fish species were correlated with both the extent of acidification and habitat diversity of the lakes. The importance of species interactions after lime treatment was suggested by a negative relationship between changes in the scores of community along the first component of the fish PCA and changes along two of the other species components between the two samplings. Despite a weak tendency towards reduced variability in species proportions as time passed since the first liming, the development of community stability, expressed as lack of change in species proportions, was insignificant.

Les effets à long terme sur des populations de poisson du traitement à la chaux de lacs acidifiés de Suède sont examinés depuis 1983 en vue de l'estimation du développement et de la stabilité des assemblages de poisson après le traitement à la chaux. Au total, 77 lacs ont été échantillonnés deux fois entre 1983 et 1988 selon des méthodes normalisées. Les lacs ont été traités à la chaux entre 1 et 16 ans avant le deuxième échantillonnage. Les variables physico-chimiques ainsi que les données sur les poissons ont été réduites par une ordination PCA et les relations qui sont apparues ont été analysées par régression linéaire et par ANOVA. Les rapports entre les caractéristiques des assemblages de poisson et les facteurs du milieu dépendaient fortement de la composition spécifique des assemblages. Le nombre et la diversité des espèces de poisson ont été corrélés au degré d'acidification et à la diversité d'habitats des lacs. L'importance des interactions entre les espèces après le traitement à la chaux était suggérée par une relation inverse entre les changements observés dans les notes attribuées aux communautés dans la première composante de PCA des poissons et les changements observés dans les notes attribuées dans les deux autres composantes, d'un échantillonnage à l'autre. Malgré une légère tendance à une réduction de la variabilité des proportions prises par chaque espèce avec le temps depuis le premier traitement à la chaux, le développement d'un équilibre au sein des communautés, exprimé par une absence de variation des proportions des communautés, était insignifiant.

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It has been emphasized that long-term monitoring programmes will be of great importance in the assessment of effects of environmental perturbation (Schindler 1988). A crucial point is the ability to distinguish between natural variation and effects of low-level perturbations. Liming may severely affect heavily acidified ecosystems. In contrast, when only slightly acidified waters are limed, or when using lime treatment preventively, effects may be obscured, from a short-term perspective, by natural variation, and an eventual change of the ecosystem is not possible to detect.

Studies of the effects of liming on freshwater fish show that liming can temporarily mitigate effects of acidification (e.g. Hultberg and Andersson 1982; Eriksson et al. 1983; Nyberg 1984; Nyberg et al. 1986a, 1986b). The main changes in fish populations are resumed recruitment and increased abundance of some species. Upon reviewing the effects of liming on the freshwater biota, Weatherley (1988) concluded that if the long-term ecological consequences of liming are to be predicted, further understanding of the function and the stability of aquatic communities is necessary.

Although lake liming has been shown to cause a considerable increase in abundance for some fish species (Nyberg et al. 1986a), it is not known whether or when a fish community stabilizes after liming. In acidified lakes, fish communities may be unstable because of reproductive failure in some species and environmental exclusion of others. However, species in species-poor lakes can compensate in number or biomass for missing species confined to more species-rich lakes of similar productivity (Tonn 1985). After liming, reproductive success, species richness, and species diversity should increase because the environmental conditions become more favourable (Odum 1981).

To assess the long-term effects of lime treatment on fish populations in Sweden, a monitoring programme began in 1983 (Appelberg et al. 1989). In the present paper, data from this programme have been used to assess the effects of liming on species composition and diversity of the fish communities. By including a large number of lakes, sampled on two occasions at different times after the addition of limestone, we are able

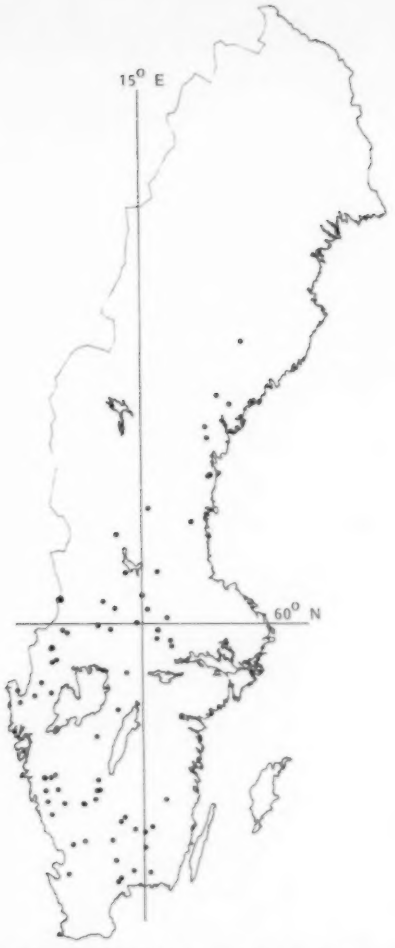

FIG. 1. Location of the 77 limed lakes sampled twice between 1983 and 1988.

TABLE 1. Physical data for the 77 lakes.

Variable	Median value	Minimum value	Maximum value
Altitude (m)	193	29	582
Area (ha)	172	15	9540
Maximum depth (m)	21	2	86
Mean depth (m)	7	1.5	32
Water retention time (yr)	2.2	0.1	45.6
Percentage littoral zone	16.6	1.9	97.0
Shoreline development	2.7	1.5	5.4

to describe the development of fish assemblages and assess their stability following lime treatment.

Material and Methods

Site Description

The studied lakes are located mainly in the southern and mideastern parts of Sweden (Fig. 1; Table 1). The frequency of occurrence of the three most abundant species, perch (*Perca fluviatilis*), roach (*Rutilus rutilus*), and northern pike (*Esox lucius*), was close to that shown by Lundberg (1899) for over 3000 Swedish lakes. However, deep, clearwater lakes inhabited by Arctic char (*Salvelinus alpinus*) and lakes inhabited by whitefish (*Coregnus* spp.) and cisco (*Coregonus albula*) were overrepresented in the present study as compared with Lundberg's figures.

All lakes were oligotrophic with low conductivity, low total phosphorus, and low water colour (Table 2). The time between first lime treatment and the first sampling varied between 2 and 13 yr (mean 6.8 yr) and the mean pH value increased by an average of 0.3 unit between the first and second samplings (Table 2). All lakes are limed repeatedly in order to avoid pH below 6.0 (Nyberg and Thörnelöf 1988). The sampling of lakes of different sizes was evenly distributed in relation to time after lime treatment.

Sampling Programme

The fish sampling programme was initiated in 1983. In total, 77 lakes were sampled twice at 3-yr intervals until 1988. All lakes were limed at least 1 yr before the second sampling. The first period in the statistical analyses includes the years 1983–85, and the second period for repeated sampling includes 1986–88.

Physical Factors

Physical factors included in the study were latitude and longitude, altitude, lake area, lake maximum and mean depth, theoretical water residence time, and the percentage littoral zone (Table 1). The latter was estimated from bathymetric maps for each lake; the bottom area shallower than 2 m was regarded as the littoral zone. Shoreline development was calculated as the ratio between the measured lake perimeter and the perimeter for a circular lake of the same area.

Water Chemistry

Data on water chemistry were obtained from the Swedish National Environment Protection Agency. Additional data from county administrative boards and the Swedish National Board of Fisheries were also included.

Data on the following factors were included in the analyses: pH, alkalinity, conductivity, water colour, total phosphorus, and total aluminium. All water analyses were performed according to Swedish standard methods (SIS 1981). Alkalinity was titrated to an endpoint of pH 5.4. Both mean and lowest recorded pH and alkalinity during the 3-yr periods preceding each fish sampling were included in the dataset. For other factors, mean values for both periods combined were used.

Lowest recorded pH, which was negatively correlated with the variance of pH after liming ($R^2 = 0.59$, $p < 0.0001$, $n = 77$, linear regression), was used as a measure of the abiotic variation after lime treatment. This means that in lakes where pH fluctuated, either within or between years, the lowest recorded pH was low.

Fish Sampling

Fish were sampled using the standardized gillnetting technique described by Degerman et al. (1988) and performed in such a way that all parts and depths of the lake were sampled. The multimesh benthic gill nets used were 42 m long and 1.5 m deep. Each gill net consisted of fourteen 3-m sections, with

TABLE 2. Time elapsed between first lime treatment and first sampling, and chemical and physical data for the 77 lakes. When values are given for the first and second samplings separately, mean values for the 3-yr period preceding a sampling are given. Other variables are given as mean values during the period 3 yr before the first sampling up to the second sampling.

Variable	Mean value	Minimum value	Maximum value
Time since first liming (yr)	6.81	2.0	13.0
Mean pH			
Before 1st sample	6.24	4.40	7.20
Before 2nd sample	6.55	5.20	7.40
Lowest recorded pH			
Before 1st sample	5.77	4.30	7.10
Before 2nd sample	6.11	4.40	7.40
Mean alkalinity (μequiv./L)			
Before 1st sample	70	0	170
Before 2nd sample	110	0	230
Minimum alkalinity (μequiv./L)			
Before 1st sample	40	0	130
Before 2nd sample	70	0	230
Temperature (°C)			
1st sample	18.3	11.0	25.4
2nd sample	18.1	13.8	23.8
Water colour (mg Pt/L)	44	5	200
Mean conductivity (mS/m)	5.2	2.0	9.7
Mean total phosphorus (μg/L)	8.1	4	32
Mean total aluminium (μg/L)	89.3	14	341

mesh sizes ranging between 6.25 and 75 mm (Hammar and Filipsson 1985).

All fish sampling was performed in July or August. Nets were set at 18:00 and raised at 08:00 the following day. Water temperature was measured at fixed depth profiles (every 2 m to 10 m depth and every 5 m below 10 m) at each sampling. The number of net sets was determined on the basis of the lake area and maximum depth sampling effort varied betwen 8 and 75 gill nets. The gillnetting was stratified by depth with the number of nets used in each depth zone in proportion to the volume of the specific zone. The depth zones were 0–2.9, 3–5.9, 6–11.9, 12–19.9, 20–34.9, 35–49.9, 50–74.9, and deeper than 75 m. The nets were randomly set within each zone.

All fish caught were identified to species and measured (total length) to the nearest millimetre. Pooled values for weight were determined for each species per net to the nearest gram. Mean values for number and biomass per net were used as measures of catch per unit effort (CPUE) for each species in each lake.

A drawback when using passive sampling gear is that water temperature strongly affects the catch statistics (Neuman 1979; Degerman and Nyberg 1989). By including temperature differences between samplings as a covariate in most analyses, some of the variation attributable to water temperature could be accounted for.

Numerical and Statistical Analyses

Data transformations

As most of the environmental variables were not normally distributed, $\log_{10}$-transformed data were used in all statistical analyses. Variables transformed were altitude, lake area, lake maximum and mean depth, residence time, water colour, conductivity, alkalinity, total aluminium, and total phosphorus. CPUE, both in numbers and weight, was normalized according to $y = \log_{10}(x + 1)$ (Degerman et al. 1988).

Reduction of environmental data

Expecting that several of the environmental variables were correlated, thereby causing collinearity, the number of variables was reduced using principal component analysis (PCA) (Rawlins 1988). For chemical variables, the average value for all 6 yr was used. After primary ordination, factors were orthogonally rotated using varimax rotation and Kaiser normalization to increase interpretability (Pielou 1984; SPSS Inc. 1988). The Kaiser–Meyer–Olkin (KMO) measure of sampling adequacy was used to test the adequacy of using PCA (Kaiser 1974). This index compares the magnitudes of the observed correlation coefficients with the magnitudes of the partial correlation coefficients. Low values (below 0.5) indicate that correlations between pairs of variables cannot be explained by other variables (Kaiser 1974). Accepting only components with eigenvalues above 1, factor scores for each lake were calculated using the regression method (lake-by-environment scores) (SPSS Inc. 1988). The regression factor scores have a variance equal to the squares multiple correlation between the estimated factor scores and the true factor values.

Hierarchical classification of species occurrence

A classification of lakes, based on fish species presence/absence, failed to give biologically interpretable results. Therefore, a classification of fish species presence/absence was performed separately on the first and second samplings. Only the 15 most frequently occurring species were included. The clustering method used was the average linkage between groups (Pielou 1984).

Ordination of lakes based on fish biomass

The species biomass of the 15 most frequently occurring species was also used to ordinate lakes by PCA. Log_{10}-transformed biomass values ($CPUE_{(weight)}$) were used; otherwise the method was similar to that for environmental variables. By including data from both the first and second sampling in the same analysis, factor scores for both samplings were calculated (lake-by-species scores).

Measure of diversity and stability

To compare species diversity among lakes, Shannon–Wiener's H was used based on the $CPUE_{(numbers)}$ of fish (Pielou 1969). An H value was calculated for each lake and sampling with all species included. After removing the variation in H that could be explained by lake area (see Rahel 1986), the number of nets used did not significantly influence species diversity (linear regression, $p > 0.05$). As an expression of the stability of the fish communities, the change in species proportions between samplings was determined for each lake (Euclidean distance). This was calculated as the square root of the sum of the squared differences between the proportions (in numbers) of each species. A stable community was defined as one in which the Euclidean distance between two samples was 0. Normalized values of Euclidean distance ($y = \log_{10}(x + 1)$) were used in all analyses.

Comparison between fish and environmental data

The importance of temperature differences between samplings was analyzed by regressing the difference in $CPUE_{(numbers)}$ for each species against the water temperature difference. Changes in $CPUE_{(numbers)}$ and $CPUE_{(weight)}$ for each fish species between sampling occasions were analyzed by paired sample t-test. The changes in CPUE were further examined by ANOVA using water temperature (2 m depth) at time of sampling as covariate.

To analyze the relationship between the fish communities and the environment on the first and second samplings, the calculated lake-by-species scores from the PCA of fish biomass (five factors) were used as dependent variables in a multiple linear regression, with the lake-by-environment scores from the ordination of abiotic variables used as independent variables. Linear regressions were also used to compare the number of species, species diversity, and Euclidean distance between samplings with the environmental PCA scores. The diversities (H) of the first and second samplings were compared using a paired sample t-test. The change in species proportions (Euclidean distance) between the two sampling occasions was analyzed both in relation to the environment and to time after lime treatment using linear regression.

The extent to which the change in factor scores of individual assemblages in the lake-by-species ordinations (for the first and second samplings) was dependent upon the time elapsed since liming (divided into four time classes) was analyzed for each principal component by ANOVA, using temperature differences between samplings as a covariate.

Results

Ordination of Lakes by Abiotic Factors

In the ordination of lakes by environment, the first four principal components, comprising 70% of the total variation, had eigenvalues above 1 (Table 3). The KMO index of adequacy was 0.69, indicating that the ordination was acceptable. The first principal component may primarily be regarded as a trophic component (Table 3). The second principal component may be seen as a geographical component. The third principal component was mainly related to acidification whereas the fourth principal component was positively related to lake area and shoreline development, i.e. a habitat diversity component (Table 3).

TABLE 3. Factor loadings for environmental principal components for the 77 limed lakes. Only loadings above 0.5 are shown.

	Principal component			
	I	II	III	IV
σ, variance accounted for (%)	29.5	18.1	14.2	8.4
Σ σ (%)	29.5	47.6	61.7	70.2
Abiotic variables				
Mean lake depth	−0.88			
Turnover time	−0.87			
Maximum lake depth	−0.85			
Littoral zone (%)	0.84			
Water colour	0.82			
Total aluminium	0.72			
Total phosphorus	0.71			
Conductivity		−0.92		
Latitude		0.86		
Altitude		0.74		
Longitude		0.60		
Mean pH			0.82	
Minimum alkalinity			0.81	
Minimum pH			0.78	
Mean alkalinity			0.73	
Lake area				0.83
Shoreline development				0.56

TABLE 4. Species occurrence on the first and second sampling occasions including all species.

Species	No. of lakes		
	1st	2nd	Diff.
Perch (*Perca fluviatilis*)	73	74	+1
Roach (*Rutilus rutilus*)	50	48	−2
Pike (*Esox lucius*)	45	43	−2
Whitefish (*Coregonus* spp)	24	25	+1
Arctic char (*Salvelinus alpinus*)	23	22	−1
Ruffe (*Gymnocephalus cernua*)	19	19	0
Cisco (*Coregonus albula*)	18	18	0
Burbot (*Lota lota*)	18	22	+4
Smelt (*Osmerus eperlanus*)	15	14	−1
Bream (*Abramis brama*)	15	17	+2
Bleak (*Alburnus alburnus*)	15	12	−3
Brown trout (*Salmo trutta*)	13	10	−3
European minnow (*Phoxinus phoxinus*)	12	12	0
Rudd (*Scardinius erythrophtalmus*)	5	5	0
Tench (*Tinca tinca*)	3	5	+2
Alpine bullhead (*Cottus poecilopus*)	3	5	+2
Bullhead (*Cottus gobio*)	3	2	−1
Stickleback (*Gasterosteus aculeatus*)	1	1	0
Ninespine stickleback (*Pungitius pungitius*)	1	0	−1
Pikeperch (*Stizostedion lucioperca*)	0	2	+2
Silver beam (*Blicca bjoerkna*)	0	1	+1
European eel (*Anguilla anguilla*)	0	1	+1

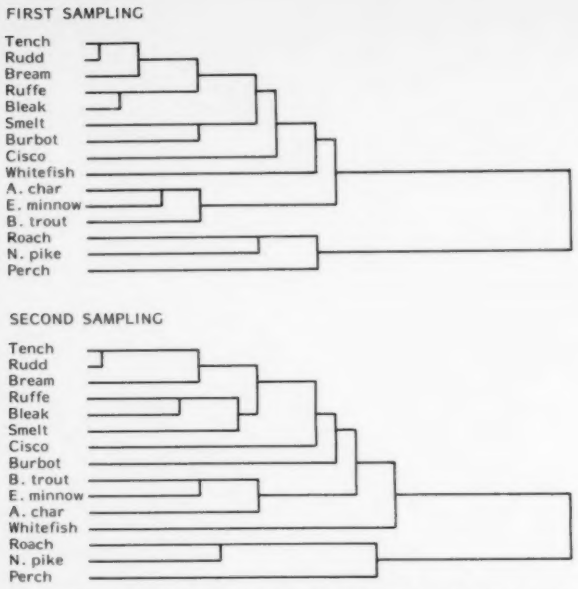

FIG. 2. Hierarchical classification of the 15 most abundant fish species using average linkage between groups clustering. The analyses were based on presence/absence data and separated between the first and second sampling occasions.

Mean pH, lowest recorded pH, and the change in pH between samplings were not correlated with the time passed since the first lime treatment (linear regression, $p > 0.05$).

Species Distribution and Composition

In total, 22 fish species were caught (Table 4). Perch was the most common species followed by roach and northern pike. Other common species were whitefish, Arctic char, ruffe (*Gymnocephalus cernua*), cisco, and burbot (*Lota lota*).

In hierarchical classification of fish species of the first sampling (1983–85), the three most widespread species, perch, roach, and northern pike, were separated from the rest of the species to form a distinct group (Fig. 2). In the second group, the coldwater species Arctic char, brown trout (*Salmo trutta*), and European minnow (*Phoxinus phoxinus*) were separated from the other species. In the further divisions, whitefish and cisco formed two separate groups. Subsequently, burbot and smelt (*Osmerus eperlanus*) were separated from tench (*Tinca tinca*), rudd (*Scardinus erythrophtalmus*), bream (*Abramis brama*), ruffe, and bleak (*Alburnus alburnus*). The result of the second sampling (1986–88) did not indicate any major changes.

Despite the fact that species relationships are complex and possibly seldom linear, the ordination of lakes by species biomass resulted in five principal components with eigenvalues above 1. The KMO index was 0.73, indicating an acceptable ordination. The total explained variation of the five components was 64% (Fig. 3).

In the first component, which explained 28% of the variation, northern pike, roach, and cisco had high positive loadings whereas Arctic char and European minnow had high negative loadings. In the second component (11%), bream, rudd, and tench had positive loadings and cisco a negative loading. In the third component (9%), smelt, burbot, ruffe, and bleak all had positive values. In the fourth component (8%), perch had a positive loading and brown trout a negative loading. In the fifth component (8%) (not shown in Fig. 3), whitefish had a negative loading.

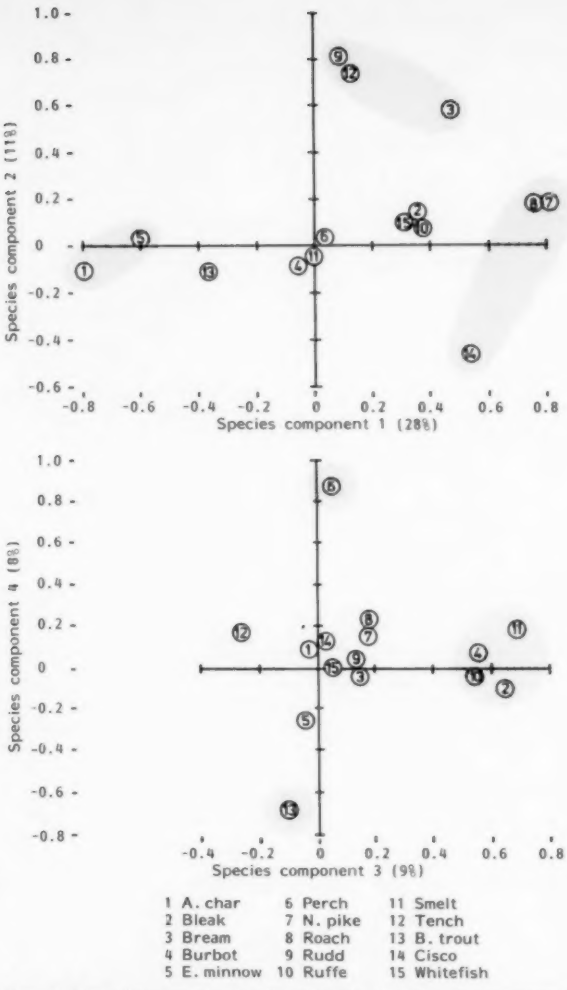

FIG. 3. Plot of the species loadings for the first four components of the ordination of lakes by species. Species within shaded areas all have loadings above 0.5 or below −0.5. Variance accounted for is given in percent for each component.

Relationship between Species Composition and Abiotic Variables

Factor scores for lakes on the first component of the species PCA were correlated positively with scores on the first and fourth components, and negatively with scores on the second component, of the environmental ordination (Table 5). Thus, assemblages with relatively high biomass of northern pike, roach, and cisco (and thus high scores on the first species component) tended to occur in lakes having high scores on the trophic and habitat diversity components and low scores on the regional component. For Arctic char and European minnow the situation was reversed.

Similarly, scores for lakes along the second species component (associated with the biomass of bream, rudd, and tench–cisco) were positively related to the trophic component and neg-

TABLE 5. Correlation matrix between the resulting lake-by-species scores after ordination of the fish biomass (PCA) on the first sampling occasion and the four environmental components. All correlation coefficients significant at the 0.01 level.

Species component	Environmental component			
	Trophic	Regional	Acidification	Habitat diversity
1	+0.41	−0.42		+0.42
2	+0.41	−0.20		
3		+0.37	+0.42	
4	−0.32	−0.49		
5				−0.44

atively correlated with the regional component. Scores along the third species component (predominance of smelt, ruffe, burbot, and bleak) were positively related to both the acidification axis and habitat diversity axis. Along the fourth species component (perch – brown trout), lakes were negatively related to both the trophic and regional components, i.e. the biomass of perch was lower and brown trout higher at high altitudes, further north, and in less productive lakes. Scores along the fifth species component (negative for whitefish) were negatively related to the habitat diversity component only, indicating that the biomass of whitefish was high in large lakes with high habitat diversity.

Changes in Relative Abundance

Despite the fact that all test fishing was performed during July and August, when water temperature was expected to be high and stable, the temperature differed between the two sampling occasions by a maximum of 9°, with a mean temperature difference of 0.3°. Temperature at the time of sampling influenced the catches positively for 3 of 15 species. For perch, the difference in temperature explained 12% of the variation in CPUE between the two sampling occasions whereas the explained variation for bream and bleak was 37 and 25%, respectively ($p < 0.05$).

The mean $CPUE_{(numbers)}$ of fish decreased from 22.3 (SD = 14.0) on the first sampling to 17.6 (SD = 12.4) on the second ($p < 0.001$). The total $CPUE_{(weight)}$ was also slightly reduced, from 1062 g/net (SD = 689) on the first sampling to 943 g/net (SD = 587) on the second ($p < 0.05$). The overall changes in number and weight could be related neither to the time elapsed since the first lime treatment nor to the change in pH between samplings. Although the $CPUE_{(weight)}$ of all fish was positively correlated with the $CPUE_{(numbers)}$ of all fish ($R^2 = 0.46$, $p < 0.001$), it was independent of the number of species ($p > 0.05$).

The major contribution to the reduction in overall CPUE was made by the two most abundant species, perch and roach. Both species showed significantly reduced numbers on the second sampling compared with the first. Perch decreased from 14.6 to 10.8 individuals/net in lakes where it occurred ($p < 0.001$), and roach declined from 8.2 to 6.8 ($p < 0.05$). The mean $CPUE_{(numbers)}$ of northern pike was also reduced, 0.18 and 0.14, respectively ($p < 0.05$). Variations in other species were insignificant; however, 8 of the 12 other species were less abundant on the second sampling compared with the first.

Changes in Species Diversity

The number of species on the first sampling was positively correlated with both the acidification and habitat diversity components of the environmental ordination (multiple linear regression, $R^2 = 0.49$, $p < 0.001$). Accordingly, 48% of the variation in Shannon–Wiener's H on the first sampling was explained by positive relationships with the habitat diversity component and the acidification component and negative relationships with the regional component ($p < 0.001$). Similar results were obtained for the index of diversity during the second sampling when 51% of the variation was explained, with the habitat diversity component being the factor of greatest importance ($p < 0.001$), i.e. species diversity was higher in nonacidified, large lakes and lakes with a relatively long shoreline. Conversely, species diversity was lower in lakes located in the north and west of Sweden and in lakes at high altitudes.

Species diversity (H) was also positively correlated with scores along the first and third species component ($p < 0.05$). This indicates that lakes dominated by roach, northern pike, and cisco as well as lakes with smelt, ruffe, burbot, and bleak were the most diverse ones as a result of a high habitat diversity. Mean species diversity increased slightly during the 3-yr period; H was slightly higher on the second sampling (mean = 1.19, range 0–2.49) compared with the first (mean = 1.12, range 0–2.27, $p < 0.05$).

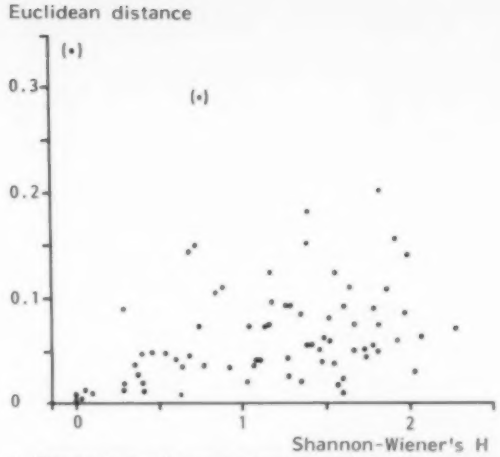

FIG. 4. Change in species proportions (Euclidean distance) between the two samplings plotted against the mean value of the species diversity (Shannon–Wiener's H) for the two samplings. The values of the Euclidean distance were $\log_{10}$ transformed. Two outliers are noted in parentheses.

Community Stability after Liming

The change in species proportions (Euclidean distance) between samplings was greater in lakes with high species diversity ($R^2 = 0.06$, $p < 0.05$; Fig. 4). Two outliers could be noted, Lake Illeråsasjön and Lake Bösjön. In the former lake, only northern pike was caught on the first sampling whereas perch was also abundant on the second sampling occasion. In Lake Bösjön, inhabited only by Arctic char and brown trout on the first sampling, there was an invasion of European minnow which increased its CPUE from 0 to 7.8 individuals/gillnet during the 3-yr period. When these lakes were excluded from the analyses, the explained variation increased to 22%. Neither the lowest recorded pH nor the change in pH between the two samplings was correlated with Euclidean distance (linear regression, $p > 0.05$).

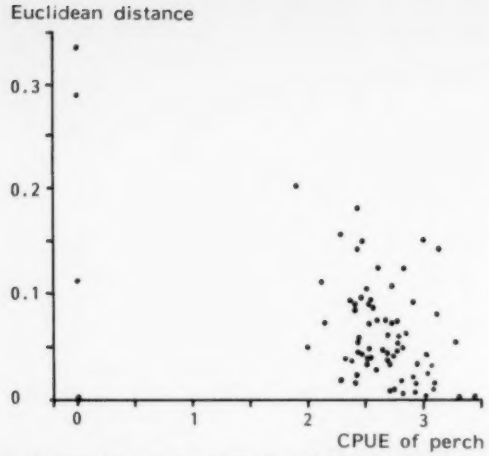

FIG. 5. Change in species proportions (Euclidean distance) plotted against the $CPUE_{(weight)}$ of perch on the first sampling. Both axes were $\log_{10}$ transformed.

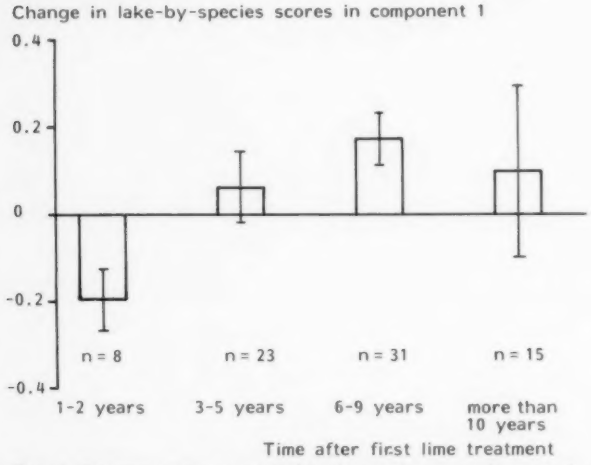

FIG. 6. Changes (mean ± SE) in lake-by-species scores between the first and second sampling occasions for the first component (roach, northern pike, cisco – Arctic char, and European minnow) in relation to time elapsed after the first lime treatment.

Of all 22 species, the change in species proportions was related only to the biomass of perch (linear regression, slope $= -0.05$, $R^2 = 0.27$, $p < 0.001$; Fig. 5). After excluding the four lakes in which perch was missing on the first sampling, the explained variation decreased to 13%, although the slope did not change. The change in abundance of perch between samplings, however, did not influence the change in species proportions ($p > 0.05$).

The changes in lake-by-species scores along the first species component (roach, northern pike, cisco – Arctic char, and European minnow) were the only ones significantly related to the time elapsed since the first lime treatment (ANOVA, $p<0.01$; Fig. 6). During the first 2 yr following liming the average score along the first component declined. This was mainly attributable to a reduction in the biomass of roach, northern pike, and cisco. This decline in average score was followed by increases (movement up the axis) during the periods 3–5 and 6–9 yr after the first lime treatment, indicating greater biomasses of roach, northern pike, and cisco.

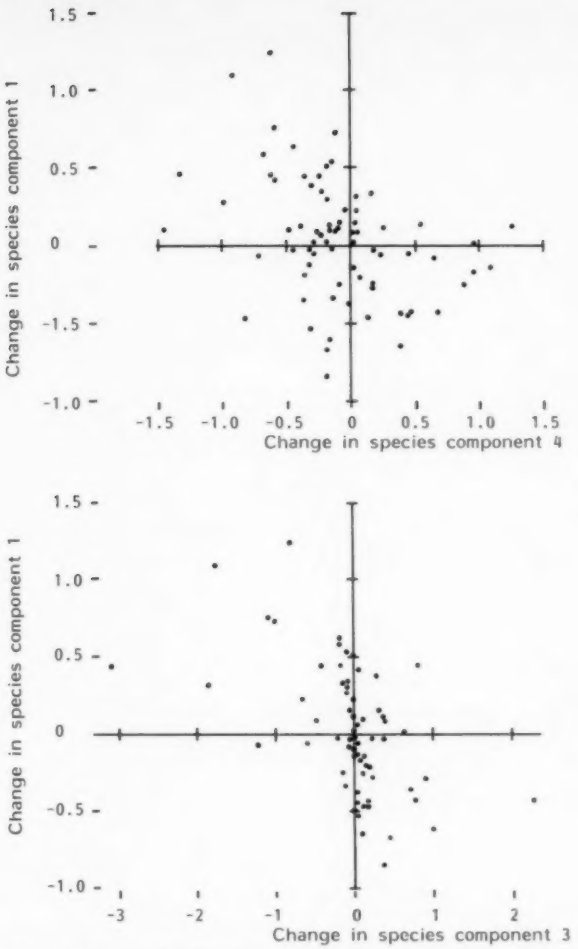

FIG. 7. Change in lake-by-species scores between the two sampling occasions. Top panel: First component (roach, northern pike, cisco – Arctic char, and European minnow) versus fourth component (perch – brown trout). Bottom panel: First component versus third component (smelt, bleak, ruffe, and burbot).

The occurrence of species interactions after lime treatment was suggested by the negative relationship between the changes in lake-by-species scores along the first species component and the change in lake-by-species scores along the third component, comprising smelt, bleak, burbot, and ruffe (slope $= -0.30$, $R^2 = 0.13$, $p < 0.001$), and the fourth species component, composed of perch – brown trout (slope $= -0.31$, $R^2 = 0.26$, $p < 0.001$; Fig. 7).

There was no significant relationship between the mean Euclidean distance (changes in species proportions) and time elapsed since the first lime treatment (Fig. 8), largely because the variation in Euclidean distance was large within years. However, after an initial increase in the first 3 yr after liming, Euclidean distances showed a weak decrease during the following years (linear regression, $p = 0.15$).

Discussion

In many recent studies, discrete grouping of fish assemblages, often based on species presence/absence data, has been

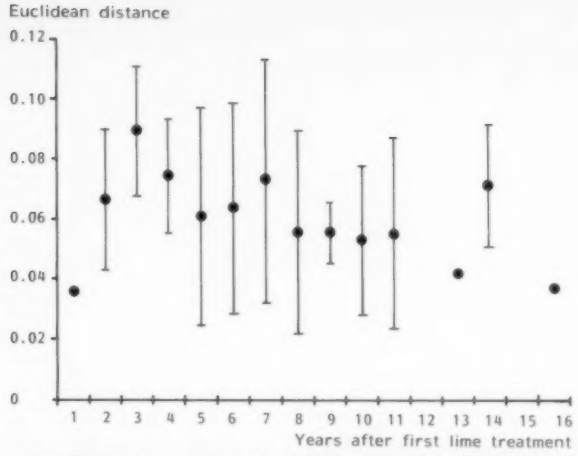

FIG. 8. Changes (mean ± SE) in species proportions plotted against time elapsed after the first lime treatment. The changes in species proportions were calculated as the Euclidean distance between the first and second sampling occasions based on fish numbers. Log_{10} transformation was used to normalize the values.

used to interpret species relationships along environmental gradients (e.g. Tonn and Magnuson 1982; Rahel 1984, 1986). In the present study, the initial use of hierarchical classification of lakes based on species presence/absence data failed to give interpretable results, and the subsequent classification of species must be interpreted with care. Species that occur frequently, such as perch, will be grouped in a single group. On the other hand, rare species will largely be grouped together. As an alternative approach to a hierarchical classification of fish assemblages, an ordination of lakes based on the biomass of the species was thought to be more relevant. According to the KMO index, the ordination used was sufficiently good (Kaiser 1974), and more refined methods for ordination of lakes were therefore excluded. With some exceptions, the resulting community gradients from the ordination agreed to a large extent with an earlier ordination of fish assemblages based on species abundance (in numbers) in 110 acidified and limed lakes (Appelberg et al. 1989). Also, the components of the fish assemblages ordination resembled the classification of species.

The decrease in total fish abundance (both in weight and number) on the second sampling was mainly attributable to a reduction in perch and roach, the most abundant species. The lack of correlation between CPUE and time elapsed after liming and with change in lowest recorded pH is possibly due to the large environmental variation among lakes. It is possible that an initial increase in fish abundance (in number) after liming, due to increased recruitment (Nyberg et al. 1986a), had ceased and that increased inter- and intraspecific competition had caused a reduction of species abundance. Such findings have been reported for other limed lakes in Sweden (Degerman and Nyberg 1989).

The changes in species composition were small. The changes of lake scores along the first principal component in the species assemblages ordination, separating lakes dominated by roach, northern pike, and cisco from those dominated by Arctic char and European minnow, were the only ones significantly related to time elapsed after first liming. Several of the species with high loadings on this component have been found to be sensitive to acid stress. Roach, for example, is one of the most acid-sensitive species among those occurring in low productive Swedish lakes (Almer 1972; Degerman and Nyberg 1989). Appelberg et al. (1989) found that both cisco and European minnow also occurred less frequently in lakes with pH recorded below 5.5. Arctic char is also regarded as acid sensitive (Nyberg et al. 1986b). However, although this species is often reintroduced after liming (Nyberg 1988), reintroductions were only performed in two of the present lakes.

Since the ordination of lake-by-species formed five uncorrelated species components, a change in biomass of a single fish species in any given lake, causing a movement along one or more of the components, need not necessarily influence the position on other components. However, the change in lake-by-species scores along the first component (roach, northern pike, cisco – Arctic char, and European minnow) between the first and second sampling was negatively correlated with both the third (smelt, ruffe, burbot, and bleak) and the fourth (perch – brown trout) components. Although these relationships may be due to different environmental optima for different species, they are probably an effect of species interactions. Several of the species comprising the first component have been proven to be important species structuring the fish assemblages. Species interactions supporting the negative relationship between the scores along the first and fourth species components are the intraspecific competition between roach and perch (Svärdson 1976; Persson 1986) and between Arctic char and brown trout (Nilsson 1978). The negative relationship between the scores along the first and third species components may involve both the interspecific competition between cisco and smelt (Svärdson 1976) and the importance of smelt as food for Arctic char (Filipsson and Svärdson 1976).

According to Wiens (1977) the stability of an ecosystem decreases during environmental perturbations, thereby reducing the impact of biotic interactions. However, coexistence in a variable environment can be just as strong and stable as in a stable environment, since environmental variability may reduce competitive exclusion (Chesson 1986). Liming acid water causes an initial perturbation of the ecosystem and a relaxation of environmental stress. This effect is greater when acidification is greater before treatment. After lime treatment the development of fish populations should mainly be regulated by the biotic interactions within the new environmental limits (Nyberg et al. 1986a; Degerman and Nyberg 1989). After the initial increase of opportunistic species with high reproductive capacity (e.g. perch), the subsequent increase is moderated, and acid-sensitive species, such as roach, cisco, and European minnow, resume their dominance. When a longer period has elapsed after liming, the fish community becomes progressively less variable. The slightly increased species diversity observed during the second sampling (the slight increase in Shannon–Wieners's H between samplings) indicates that the lakes are slowly becoming more diverse after liming.

Species composition in the limed lakes is probably less stable compared with nonacidified systems as a result of repeated lime treatment and pulses in pH during snowmelt (Hultberg 1977; Dickson 1980; Molot et al. 1990). If the lakes are not limed sufficiently, pH drops and recruitment failure in sensitive species may occur (Nyberg et al. 1986a). The positive relationship between the acidification component and species diversity indicates that low pH is still important after liming. However, as Euclidean distance (the change in species proportions) was not related to the lowest recorded pH (i.e. the variation in pH after liming, see Material and Methods), the effects of a fluctuating

pH after liming were possibly less pronounced in the lakes studied.

In general, the change in species proportions between samplings (Euclidean distance) was related to species diversity: the greater was the species diversity, the larger were the changes in species proportions. This relationship is in agreement with earlier hypotheses suggesting that diverse communities are in general less stable to environmental perturbations compared with simple ones (e.g. May 1974; Roughgarden 1989). However, two exceptions to this rule were noted (Fig. 4): Lake Illeråsasjön and Lake Bösjön. In both lakes the number of species was low and a new species was caught in relatively large numbers during the second sampling, perch and European minnow, respectively.

There was no clear-cut relationship between Euclidean distance and time elapsed after the first liming. According to earlier studies of the effects of environmental perturbations on aquatic ecosystems (Boesch and Rosenberg 1981), one would have expected increased changes in the species proportions for the first few years, followed by a slow restabilization. Although the nonsignificant decrease in mean Euclidean distance after the third year following lime treatment could be interpreted as a decreased variability of the species proportions, this pattern was not statistically significant. These results may be contrasted with those of Pimm and Redfearn (1988) who found that the variability of population densities increases in relation to the number of years included in the calculations. This may be attributed to the nature of the environmental variation.

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Effects of Ageing Errors on Recruitment Time Series Estimated from Sequential Population Analysis

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Bradford, M. J. 1991. Effects of ageing errors on recruitment time series estimated from sequential population analysis. Can. J. Fish. Aquat. Sci. 48: 555–558.

Ageing errors can introduce considerable bias in the time series of recruitment estimated from a sequential population analysis. Simulation results indicate that mild ageing errors can halve estimates of the variance of recruitment and can introduce potentially important autocorrelations in recruitment time series. Underageing resulting from the use of unvalidated ageing techniques can affect recruitment estimates sufficiently to severely hinder studies of environmental influences on recruitment. As an additional sensitivity analysis, researchers should consider recalculating recruitment after correcting catch data for ageing errors.

Les erreurs de détermination de l'âge peuvent introduire un biais considérable dans les séries temporelles de recrutement déterminées à partir d'une analyse de population séquentielle. Les résultats d'une simulation révèlent que de faibles erreurs de détermination de l'âge peuvent réduire de moitié les estimations de la variance du recrutement et peuvent introduire des autocorrélations potentiellement importantes dans les séries temporelles de recrutement. Des âges sous-estimés à cause de techniques de détermination de l'âge non validées peuvent suffisamment influer sur les estimations du recrutement pour fortement gêner les études des influences environnementales sur le recrutement. À titre d'analyse de sensibilité supplémentaire, les chercheurs devraient considérer un recalcul du recrutement après avoir corrigé les données sur les prises des erreurs de détermination de l'âge.

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As catch-at-age records accumulate for many commercial fisheries, it is becoming more popular for research on year-class variability to use recruitment abundances estimated from age-structured stock reconstruction models (e.g. Shepherd et al. 1984; Myers and Drinkwater 1989). Probably the most commonly used techniques to estimate cohort abundance are sequential models, frequently referred to as cohort analysis or sequential or virtual population analysis (SPA, VPA; reviewed by Megrey 1989). For studies of recruitment variation, these techniques have the desirable property that errors in the input parameter F_t, the terminal fishing mortality, diminish as the reconstruction goes backwards to the youngest age (Pope 1972). However, the input of an incorrect M, the natural mortality rate, can produce biased estimates or spurious time trends in reconstructed recruitment (Sims 1984; Bradford and Peterman 1989; Lapointe et al. 1989; Rivard 1989). Rarely, however, are the recruitment estimates used in environmental studies subjected to sensitivity analysis with respect to these input parameters.

In this paper, I quantify the effects of ageing errors on the variability and autocorrelation in recruitment time series. Various authors (e.g. Hollowed et al. 1987; Myers and Drinkwater 1989) have mentioned that this source of error could affect correlational studies of recruitment variation, and Rivard (1989) has shown that ageing errors can reduce the extremes of recruitment. In none of these papers was the magnitude of this effect quantified. Given that most ageing techniques are not validated, and can be subject to substantial error and bias (Beamish and McFarlane 1983), their potential effects on abundances estimated by stock assessment models need to be carefully considered (Powers 1986; Lai and Gunderson 1987; Tyler et al. 1989).

Methods

To assess the effects of ageing error, I first simulated a "true" fish population, removed catch from the population, and applied a matrix of ageing errors to the catch data. The modified catch data was used in an SPA and the estimated recruitment was compared with the "true" simulated recruitment.

I simulated a stochastic stationary time series of "true" age 1 recruits using log-normal distribution around a mean of 10 (i.e. 22 026 fish). Recruitment is frequently skewed in distribution, and a log-normal distribution has been justified on both empirical and theoretical grounds as adequately describing recruitment variability (Hennemuth et al. 1980; Peterman 1981). The variance of log recruitment was varied from 0.0625 to 2.25 in different runs, similar to the range found in Hennemuth et al. (1980). The Baranov catch equation was used to generate a catch-at-age matrix (see Bradford and Peterman (1989) for details). The simulated population had 10 fished ages, with the partial recruitment to the fishery set at 0.5 for the youngest age and 1 for all older ages. Fishing and natural mortality rates were set at 0.25

Two matrices of ageing errors were used to generate an estimated catch matrix from the "true" catch data (Table 1). The errors matrices represent two alternative scenarios, reflecting differing degrees of accuracy and precision in the ageing technique. In the first case, ages and determined relatively accurately, although there is some bias at the older ages. This error

TABLE 1. Two matrices of ageing errors applied to the simulated catch-at-age matrix. The upper matrix emulates a largely unbiased ageing method, while the lower matrix is heavily biased to underageing in the older age-classes.

True age	Age-class assigned									
	1	2	3	4	5	6	7	8	9	10
1	0.95	0.05	—	—	—	—	—	—	—	—
2	0.05	0.90	0.05	—	—	—	—	—	—	—
3	0.03	0.07	0.85	0.05	—	—	—	—	—	—
4	—	0.03	0.07	0.85	0.05	—	—	—	—	—
5	—	—	0.03	0.10	0.80	0.07	—	—	—	—
6	—	—	—	0.03	0.10	0.80	0.07	—	—	—
7	—	—	—	—	0.03	0.15	0.75	0.07	—	—
8	—	—	—	—	—	0.03	0.15	0.75	0.07	—
9	—	—	—	—	—	—	0.08	0.15	0.70	0.07
10	—	—	—	—	—	—	—	0.10	0.20	0.70
1	0.90	0.10	—	—	—	—	—	—	—	—
2	0.10	0.85	0.05	—	—	—	—	—	—	—
3	0.03	0.10	0.80	0.07	—	—	—	—	—	—
4	—	0.03	0.15	0.75	0.07	—	—	—	—	—
5	—	—	0.08	0.15	0.70	0.07	—	—	—	—
6	—	—	—	0.10	0.25	0.60	0.05	—	—	—
7	—	—	—	0.05	0.15	0.25	0.50	0.05	—	—
8	—	—	—	—	0.05	0.20	0.30	0.40	0.05	—
9	—	—	—	—	0.05	0.15	0.20	0.25	0.30	0.05
10	—	—	—	—	0.05	0.15	0.20	0.20	0.20	0.20

matrix is more accurate than those of either Rivard (1989) or Tyler et al. (1989). The second matrix is modelled after Tyler et al. (1989) and represents an unvalidated ageing method with substantial underageing of older fish.

The estimated catch matrix was used in Pope's (1972) SPA to generate a time series of estimated recruitment. Details of the various equations are given in Bradford and Peterman (1989) and will not be repeated here, except to note that I used the unbiased values of M and F_t in the SPA, so that without ageing errors, recruitment values derived from SPA were within 2% of the true values.

In the simulations, I used only complete cohorts, in which all fished ages were present to avoid time-trend effects associated with the most recent incomplete cohorts (Bradford and Peterman 1989). For each parameter combination, I simulated 100 sets of 45 complete cohorts, but used only the central 25 in the SPA to avoid edge effects in the estimated catch matrix. I calculated the recruitment variance and the serial autocorrelation coefficient for each run and found the median over the 100 trials.

To quantify the effects of ageing errors on correlations with environmental factors, I also generated an environmental variable that was correlated with true recruitment with an r of 0.71 (i.e. 50% of recruitment variation explained). In the various runs, I calculated the correlation between this environmental factor and the estimated recruitment from the SPA.

Results and Discussion

Ageing errors can cause a substantial reduction in the estimated interannual variability in recruitment. Even with the mild ageing errors, this reduction in variance ranged from 35% for simulations with low recruitment variability to 50% for more variable recruitment (Fig. 1). Stronger ageing errors reduced the estimated variances to one third of their "true" values (circles, Fig. 1). The median autocorrelation coefficient increased

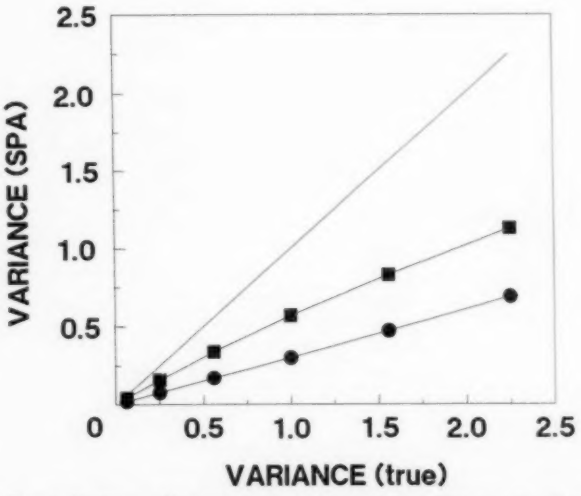

FIG. 1. Variance of log recruitment estimated from SPA as a function of the true log recruitment variance. Squares indicate results from using the matrix of mild ageing errors in Table 1 and circles are for severe ageing errors. Plotted are the medians of one hundred 25-yr runs and the 1:1 line.

with recruitment variability and ranged from 0.10 to 0.30 for both matrices of ageing errors (Fig. 2).

The matrix of mild ageing errors had only a slight effect on the correlation between log estimated recruitment and the simulated environmental factor (Fig. 2). The correlation between the environmental factor and true recruitment was 0.71, and the coefficient fell by only 0.05–0.10 when the correlation was calculated using estimates of recruitment from SPA with mild ageing errors. In contrast, recruitment estimates from SPA using the error matrix of the unvalidated ageing method reduced the correlation coefficient to below 0.40: the proportion of

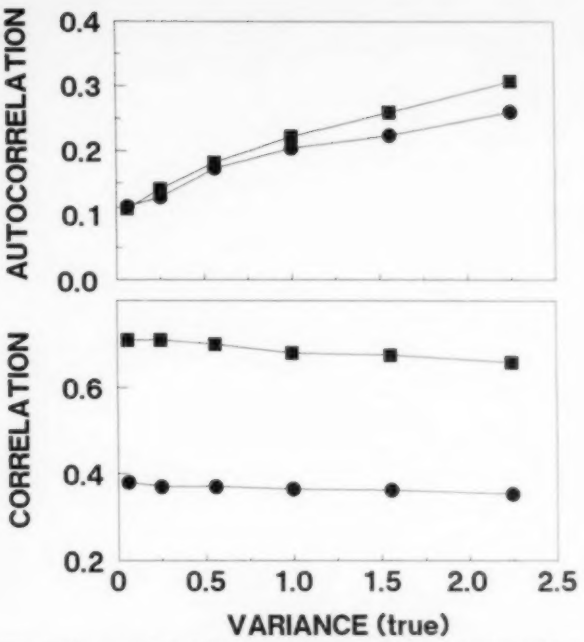

FIG. 2. Top panel: Serial autocorrelation coefficient of estimated log recruitment with symbols as in Fig. 1. Bottom panel: Correlation between a simulated environmental factor and estimated log recruitment with symbols as in Fig. 1. The correlation between the environmental factor and the log of true recruitment was 0.71. Plotted are the medians of one hundred 25-yr runs.

recruitment variance explained by the environmental factor decreased from 50% to less than 15%.

The effects I document here are the result of misclassification of fish from one cohort into adjacent year-classes in the catch matrix. When recruitment is highly variable, an abundant year-class will contribute, through ageing errors, many more fish to the adjacent weaker cohorts than it will receive from them (Rivard 1989). After SPA is conducted on the full cohort, the accumulation of this effect across all ages will tend to increase abundances of weak year-classes and reduce strong ones. This redistribution caused by ageing errors also generates the autocorrelation in recruitment time series shown in Fig. 2. The serial autocorrelation coefficient is not increased by my matrix of strong ageing errors because although the misclassification rate is higher, fish are placed in many other cohorts, not just the adjacent ones.

The impact of ageing errors on estimated recruitment has at least two implications for the study of year-class variability. First, the variability in recruitment may be greatly underestimated by reconstructed abundances: researchers simulating the recruitment process in biological or management models should consider inflating their estimated variances to account for the ageing error effects. Inferences about variability from comparisons of different species (e.g. Rothschild and DiNardo 1987) should also account for the differential effects of ageing errors in the various stock reconstruction methods used. Second, the use of unvalidated, biased ageing methods can severely hamper efforts to test hypotheses of environmentally based recruitment variation, although this effect may not be severe if the ageing technique is reasonably accurate.

The average autocorrelation coefficient generated by ageing errors is not large; however, it may artificially raise the statistical significance of tests of autocorrelation hypothesized to be biologically based. In some cases the spurious autocorrelation can be much stronger depending on the exact sequence of recruitment: for example, in the 100 runs with the recruitment variance set at 1.0, coefficients as high as 0.54 were generated. The autocorrelation coefficient will be stronger if the rate of misclassification of fish into the immediately adjacent cohorts is greater than the values in Table 1.

Recruitment researchers should consider correcting their catch-at-age matrix for ageing errors to determine the robustness of their conclusions to this source of error, especially if an unvalidated ageing technique has been used. This will increase the contrast in the recruitment estimates and may eliminate the need to take remedial measures to correct for the autocorrelation in the time series. If a matrix of ageing errors from an age validation study (i.e. Pikitch and Demory 1988) is available, the true catch matrix, C, can be reconstituted by the equation

$$C = C' E^{-1}$$

where C' is the estimated catch-at-age matrix arranged by years and E^{-1} is the inverse of the ageing error matrix (e.g. Table 1). More likely, the error matrix will have to be estimated from a subjective assessment of the accuracy of the ageing technique. Hoenig and Heisey (1987) discussed this and other techniques for correcting age data.

In summary, the pervasiveness of serious inaccuracies in ages estimated by traditional techniques (Beamish and McFarlane 1983; Pikitch and Demory 1988), and their effects on recruitment estimated by SPA, suggests that research on year-class variation should incorporate sensitivity analyses involving ageing errors. Although recruitment estimates from SPA have usually been considered to be fairly accurate, the results presented here as well as the papers cited in the introduction indicate that this assumption needs to be tested. These effects must also be evaluated with other methods of estimating catch age compositions (e.g. Fournier 1983) and the newer nonsequential stock reconstruction models (Megrey 1989).

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Infestation by Brood Symbionts and Their Impact on Egg Mortality of the Red King Crab, *Paralithodes camtschatica*, in Alaska: Geographic and Temporal Variation

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Egg masses of 772 red king crab, *Paralithodes camtschatica*, were sampled to determine the prevalence, intensity, and patterns of cooccurrence of brood symbionts from 28 Alaskan localities. *Carcinonemertes regicides* and three other undescribed nemertean egg predators were recovered from many localities, as were an undescribed turbellarian and an amphipod, *Ischyrocerus* sp. A widespread outbreak of nemerteans occurred in the 1983–84 and 1984–85 red king crab brooding seasons. At some locations, nearly all of the eggs were consumed in the 1983–84 brood season. Feeding of *C. regicides* on eggs was documented in vitro and these worms caused substantial egg mortality at many locations. The amphipod was also an egg predator and may have had a significant impact at three locations. The turbellarian did not kill eggs. From the seasonal pattern of *C. regicides* infestation at Kachemak Bay, we postulate an abbreviated life cycle and autoinfection for *C. regicides*. Such life history features may have contributed to the peak intensities observed late in the 1983–84 and 1984–85 brooding seasons. At some localities, heavy brood mortality may reduce or eliminate recruitment of some year classes to the fishery.

Les masses d'oeufs de 772 crabes royaux rouges *Paralithodes camtschatica* ont été échantillonnées afin de déterminer la fréquence, le degré d'infestation et les régimes de coexistence de symbiotes à 28 endroits de l'Alaska. *Carcinonemertes regicides* et trois autres némertiens inconnus, prédateurs des oeufs de crabe, ont été découverts à de nombreux endroits, ainsi qu'un turbellarié inconnu et un amphipode du genre *Ischyrocerus*. Une flambée générale de némertiens s'est produite au cours des saisons de reproduction du crabe royal rouge en 1983–1984 et 1984–1985. À certains endroits, presque tous les oeufs ont été dévorés au cours de la saison 1983–1984. La prédation des oeufs de crabe par *C. regicides* a été étudiée *in vitro*; ces vers sont la cause d'un taux élevé de mortalité des oeufs à de nombreux endroits. L'amphipode *Ischyrocerus* sp. est aussi un prédateur des oeufs et peut avoir eu un important impact à trois endroits. Le turbellarié n'a pas dévoré les oeufs. D'après le régime saisonnier d'infestation de *C. regicides* dans la baie Kachemak, les auteurs formulent l'hypothèse que le cycle vital de *C. regicides* est raccourci et qu'il y a auto-infection. Ces caractéristiques du cycle vital peuvent avoir contribué aux degrés d'infestation élevés observés vers la fin des saisons de reproduction de 1983–1984 et 1984–1985. À certains endroits, un taux de mortalité élevé des oeufs de crabe peut réduire ou éliminer le recrutement de certaines classes d'âge à la pêche.

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Over the last three decades the red king crab, *Paralithodes camtschatica*, from Alaska has provided one of the most valuable crab fisheries in the world (Otto 1981). In the 1980–81 season, 81 200 t of red king crab was harvested, the third highest yield in the history of the fishery. Three years later (1983–84) the harvest declined precipitously to 1000 t, the lowest catch in over 30 yr. Six of 11 Alaska Department of Fish and Game (ADF&G) management areas were completely closed to commercial crab fishing in 1983.

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Near-term recovery of these stocks cannot presently be predicted (Blau 1986).

Fishery biologists from the ADF&G and the U.S. National Marine Fisheries Service (NMFS) have monitored aspects of red king crab biology using annual surveys in various management areas for 15 yr. Visual observations on the size (reported as percentage full clutch) and state of crab egg clutches have been a regular component of these surveys (Blau 1986). Fertilized eggs (embryos) are usually oviposited in the spring (March to May) and are brooded on pleopods under the abdomen of the female crab for 11–12 mo. Hatching precedes the annual molt of the female in the following March or April (Powell and Nickerson 1965). The ADF&G biologists from Homer noted that the egg clutches of red king crabs from Kachemak Bay, in the Cook Inlet Management Area, were much smaller in November 1982 and January 1983 than were clutches examined in July 1982. Of 143 females collected in November 1982 and January 1983, the clutches of 66% were rated less than 30% full clutch (G. C. Powell, unpubl. obs.). Although some living embryos were still present in these clutches and appeared to be developing normally, many embryos were dead; often only their empty egg membranes remained attached to the pleopods. Further examination revealed that nemertean and turbellarian worms were abundant in these egg masses (Wickham et al. 1985; Blau 1986). The nemerteans included several undescribed species of *Carcinonemertes* and related undescribed genera (Wickham and Kuris 1988; Gibson et al. 1990). A new species, *C. regicides*, was the most abundant of these (Shields et al. 1989). All of the known species in this genus are symbionts of decapod crustaceans and feed on the eggs of their host (Wickham and Kuris 1985). One species, *C. errans*, has caused substantial egg mortality and has been implicated in the prolonged nonrecovery of the Dungeness crab, *Cancer magister*, fishery in central California (Wickham 1979, 1986; Kuris and Wickham 1987).

A sampling program was begun in 1983, over a large portion of the geographic range of *P. camtschatica*, to investigate the decline observed in some red king crab stocks, coincident with reports of massive egg mortalities and high-intensity infestations of nemerteans. Our goal was to determine the role of *Carcinonemertes* with respect to crab egg losses and evaluate its occurrence and impact over the range of the red king crab in Alaska. Firstly, clutch samples were collected over as broad a geographic range of the red king crab in Alaska as feasible. Egg mortality was quantified, and clutch symbionts were identified and enumerated. Relative contributions of the several symbionts to egg mortality were assessed. To study the seasonality of egg mortality, progressive embryo losses were documented for the red king crab through the brooding season in Kachemak Bay. Lastly, the role of *C. regicides* as an egg predator was established by laboratory observations including an experimental study of egg mortality in captive female crabs.

Materials and Methods

Adult female red king crabs were captured during 1983–85 over a broad geographic range in eight ADF&G king crab management areas: Southeastern Alaska, Cook Inlet (Kachemak and Kamishak bays), Kodiak Island, Alaska Peninsula, Dutch Harbor, Adak, Bristol Bay, and Norton Sound (Fig. 1). Females were caught either in baited king crab pots or in 400 eastern otter trawls primarily on ADF&G or NMFS surveys, which were generally conducted in the summer. Females were occasionally obtained from fishermen during various commercial seasons. Eighteen male and 12 nonovigerous female crabs were examined for nemerteans at Seward and Juneau.

To provide a sample to quantify egg mortality and the abundance of nemertean worms and other symbionts, the fourth pleopod of each female crab was excised at its base and preserved immediately in a vital containing 5% formalin in seawater (FSW). Of the six pleopods present, the fourth was chosen because it is located near the center of the clutch. The second to fifth pleopods carry most of the eggs (Marukawa 1933). A comparison of worm intensity among pleopods of the yellow rock crab, *Cancer anthonyi*, found that a sample of a single pleopod was a good representation of overall intensity and also of crab fecundity (Shields et al. 1990a). Carapace length, estimate of percent clutch size, depth, and location of capture were recorded for each female sampled. Percent clutch is a visual estimate of the percentage of the maximum volume of eggs that a female of such a size could carry (Blau 1986). It provides a rough estimate of fecundity (Shields et al. 1990b). Collections generally consisted of 5–30 pleopods from each management area surveyed during the summer. Replicate samples of 10 pleopods per month for several months each year were taken in Kachemak Bay, in the Cook Inlet Management Area. Seasonal sampling also occurred around Kodiak Island as additional nonsummer surveys became available. After January 1985, sampling at Kachemak Bay was randomized so that every tenth crab collected was sampled. The individual collection sites within the ADF&G king crab management areas sampled are listed in Tables 1 and 2 and are shown in Fig. 1 and 2.

To quantify nemertean infestation intensity and egg mortality on individual crabs, the symbionts present in a pleopod sample were extracted by agitation of the pleopod, identified, counted, and preserved in FSW. Manual separation of the eggs from six of these pleopods showed that over 99% of the worms were obtained by the agitation method. If the number of extracted worms exceeded about 2000, a subsampling procedure was used to estimate the number of worms per pleopod sample. The worms were poured into a petri dish with a 1-cm^2 grid. Worms were counted in six squares. The mean number of worms per square centimetre was then multiplied by the area of the dish (square centimetres) for the estimated total number of worms per pleopod. After the worms were separated from the eggs, all of the egg-bearing setae of each sampled plepod were carefully removed from the pleopod and a subsample of approximately 1000 eggs was counted and assessed for egg mortality as in Wickham (1979). Crabs whose clutches were in the process of hatching, or had already hatched, were excluded from this analysis, as egg mortality could not be distinguished from hatched eggs. Intact eggs containing normally developing embryos were counted as live, while eggs containing abnormal embryos, or eggs partially or completely devoid of their contents, were counted as dead. Abnormal eggs included opaque eggs, presumably infected with fungi, and eggs whose developmental stage was markedly retarded compared with the rest of the brood. In four samples from the Kodiak Management Area, frayed or broken funiculi, indicating detachment of eggs, were numerous (see Table 2). In these samples the mortality estimate included the count of such funiculi. Egg mortality was expressed as a percentage of the number of dead eggs per total number of counted eggs. Samples from 765 red king crabs (*Lithodes aequispina*) were analyzed in this manner.

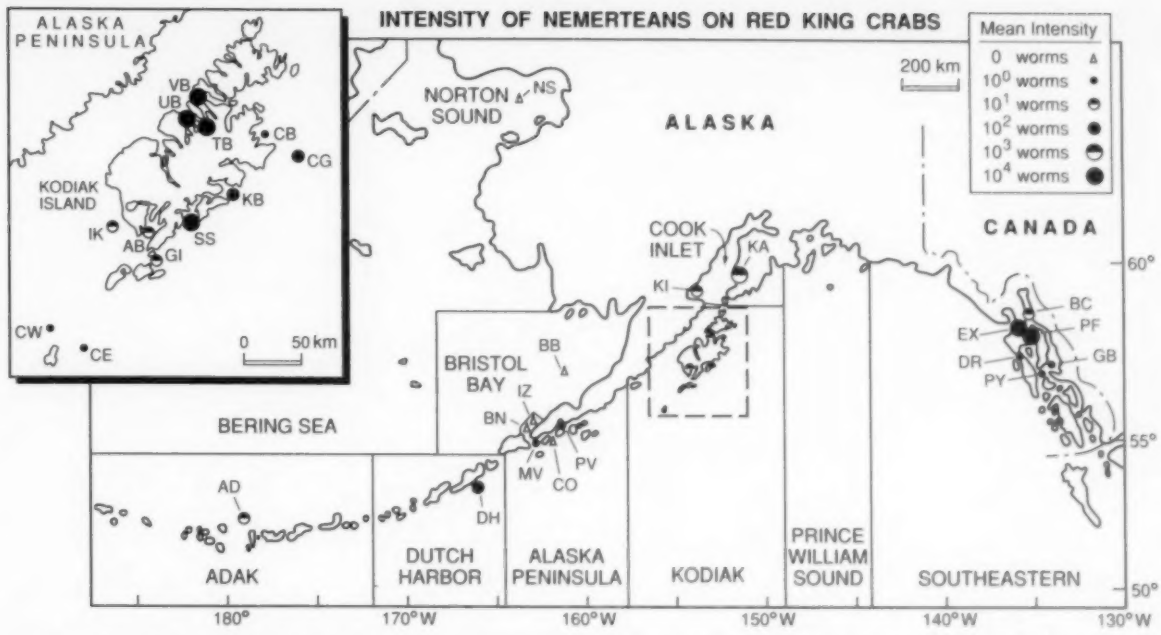

FIG. 1. Geographic distribution and intensity of *Carcinonemertes regicides* in the egg masses of red king crabs, *P. camtschatica*, in Alaska. Management areas are labelled and their boundaries are demarcated. Collecting site abbreviations are coded as in Table 1. Intensity ranges over five orders of magnitude as coded in the upper right-hand corner. Samples collected early in the brooding season (April to May) when few worms were present and egg mortality was low were omitted (see Table 1). Inset enlarges collecting sites in the Kodiak Island Management Area (broken box).

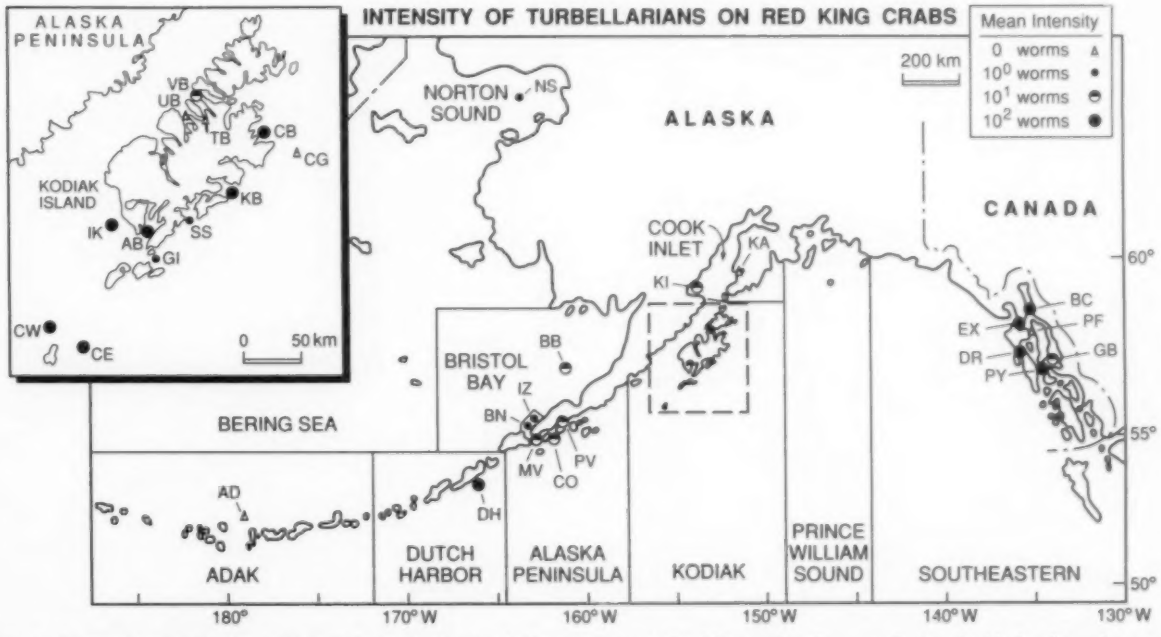

FIG. 2. Geographic distribution and intensity of turbellarians in the egg masses of red king crabs, *P. camtschatica*, in Alaska. Intensity ranges over three orders of magnitude as coded in the upper right-hand corner. See Table 1 for locality codes and Fig. 1 for other details.

In the laboratory of the Seward Marine Center, an experimental study of egg mortality compared egg losses on infested ovigerous female crabs from Kiliuda Bay and Uganik Bay (Kodiak Island) with egg losses on uninfested crabs from Kamishak Bay (Cook Inlet). All of these crabs were collected in the spring and summer of 1984. Sample sizes were 7, 22, and 20 crabs, respectively. Crabs from each location were maintained separately in flowing seawater at 6–11°C with a salinity of 31–

33 ppt. Every 30 d for 120 d, a random sample of eggs was removed from the pleopods and 300 eggs were counted. The proportion of dead eggs (empty shells or opaque embryos) and the number of nemerteans present were recorded. Additional observations on worm behavior and feeding were made in vitro.

The terms prevalence and mean intensity are defined in Margolis et al. (1982). Briefly, prevalence is the proportion of infested individuals in the host population, and mean intensity is the mean number of symbionts per infested host.

Statistical analyses were computed with the aid of SAS Institute, Inc. (1982) as per Sokal and Rohlf (1981). Correlation analyses were run on data with and without log transformation. A value of $P < 0.05$ was accepted as significant.

Results

Geographic Variation of Brood Mortality

Egg mortality increased during the brooding season (see below); thus, geographical comparisons were best made in the middle of or late in the brooding season (after July). Brood mortality exhibited considerable geographic variation (Tables

TABLE 1. Mortality of eggs of the red king crab, *P. camtschatica*, and prevalence (percentage of crabs infested) and mean intensity (number of symbionts per pleopod) ($\bar{X} \pm$ SD) of symbiotic nemerteans, turbellarians, and amphipods from various Alaskan locations (see Table 2 for details in the Kodiak Island Management Area). *N* is sample size.

Management areas and collection sites	Date (mo/yr)	*N*	Crab egg mortality (%)	*C. regicides*		Nemertean form 4		Nemertean form 5		Turbellaria spp.		*Ischyrocerus* sp.	
				Prevalence (%)	Intensity ($\bar{X} \pm$ SD)	Prevalence (%)	Intensity ($\bar{X} \pm$ SD)	Prevalence (%)	Intensity ($\bar{X} \pm$ SD)	Prevalence (%)	Intensity ($\bar{X} \pm$ SD)	Prevalence (%)	Intensity ($\bar{X} \pm$ SD)
Southeastern Alaska													
Barlow Cove (BC)	6/83	5	0.4 ± 0.3	100	48 ± 15	60	36 ± 14	40	32 ± 42	100	167 ± 145	40	2 ± 1
Deadman's Reach (DR)	6/83	5	0.4 ± 0.4	100	11 ± 5	0	—	100	11 ± 5	100	392 ± 327	0	—
Excursion Inlet (EX)	6/83	3	78.3 ± 15.3	100	10 248 ± 5950	100	6041 ± 5372	0	—	33	433	33	1
Gambier Cove (GB)	6/83	5	0.5 ± 0.6	60	4 ± 3	0	—	60	4 ± 2	100	56 ± 51	0	—
Port Frederick (PF)	6/83	7	72.9 ± 35.5	100	18 522 ± 15 006	57	6693 ± 2186	0	—	0	—	0	—
Pybus Cove (PY)	6/83	5	0.0 ± 0.0	60	7 ± 7	0	—	60	7 ± 5	100	237 ± 268	0	—
Cook Inlet													
Kachemak Bay (KA)	2/83	9	54.1 ± 33.3	100	347 ± 276	0	—	0	—	22	178 ± 189	33	19 ± 6
	7/83	10	47.5 ± 40.4	100	2008 ± 2286	0	—	0	—	0	—	0	—
	8/83	11	87.3 ± 24.6	100	2591 ± 2616	0	—	0	—	0	—	0	—
	10/83	15	95.6 ± 16.8	100	2712 ± 2100	0	—	0	—	0	—	13	8 ± 3
	3/84	10	0.1 ± 0.2	10	1	0	—	0	—	0	—	0	—
	4/84	10	0.1 ± 0.2	20	3 ± 3	0	—	0	—	0	—	0	—
	5/84	5	0.1 ± 0.3	0	—	0	—	0	—	0	—	0	—
	6/84	20	1.0 ± 1.1	100	345 ± 419	0	—	0	—	0	—	0	—
	9/84	19	59.2 ± 20.7	100	1229 ± 1232	0	—	0	—	0	—	10	1 ± 0
	11/84	20	45.4 ± 18.8	100	217 ± 224	0	—	0	—	0	—	10	5 ± 1
	4/85	20	—[a]	0	—	0	—	0	—	0	—	45	6
	7/85	30	0.4 ± 0.4	100	17 ± 21	0	—	0	—	0	—	0	—
	11/85	14	6.7 ± 13.7	100	28 ± 15	0	—	0	—	0	—	21	1 ± 0
Kamishak Bay (KI)	6/83	25	2.1 ± 6.5	88	23 ± 34	0	—	0	—	0	—	0	—
	6/84	29	0.4 ± 0.7	31	6 ± 5	0	—	0	—	55	12 ± 15	0	—
Alaska Peninsula													
Bechevin Bay (BN)	9/83	5	0.4 ± 0.8	0	—	0	—	0	—	60	7 ± 10	0	—
Cold Bay (CO)	8/84	5	1.6 ± 2.5	0	—	0	—	0	—	80	58 ± 73		
Izembek Lagoon (IZ)	9/83	10	0.2 ± 0.4	0	—	0	—	0	—	75	8 ± 11	0	—
Morshovoi Bay (MV)	7/84	10	0.6 ± 0.4	0	—	70	1 ± 1	0	—	100	37 ± 35	0	—
Pavlof Bay (PV)	9/83	10	0.8 ± 1.2	0	—	30	1 ± 0	0	—	100	21 ± 14	0	—
	8/84	10	0.2 ± 0.1	0	—	30	5 ± 3	0	—	100	25 ± 23	0	—
Dutch Harbor (DH)	10/83	10	13.3 ± 24.0	80	20 ± 21	40	14 ± 15	30	2 ± 2	100	142 ± 137	10	4
	8/84	22	37.1 ± 39.7	96	1976 ± 3968	5	10	23	29 ± 35	46	311 ± 417	9	4 ± 4
	8/85	14	30.3 ± 30.8	100	1053 ± 2047	77	1509 ± 2268	0	—	43	369 ± 800	7	4
Adak (AD)	12/83[b]	8	6.1 ± 7.5	0	—	25	2 ± 1	50	62 ± 35	75	41 ± 67	0	—
Bristol Bay (BB)	6/84	11	1.9 ± 1.3	0	—	0	—	0	—	0	—	0	—
	8/84	9	1.3 ± 1.9	0	—	0	—	0	—	0	—	0	—
	9/84	19	0.3 ± 0.3	0	—	0	—	0	—	79	33 ± 33	0	—
	6/85	28	0.0 ± 0.0	0	—	0	—	0	—	10	11 ± 12	7	1 ± 0
Norton Sound (NS)	8/83[c]	28	0.0 ± 0.0	0	—	0	—	0	—	0	—	0	—
	8/84	30	0.2 ± 0.3	7	1 ± 0	0	—	0	—	3	11	0	—
	7/85	19	0.0 ± 0.0	0	—	0	—	0	—	0	—	0	—

[a]Egg mortality could not be quantified because eggs were hatching in this sample.
[b]Includes samples from 11/83.
[c]Includes samples from 6/83.

TABLE 2. Mortality of eggs of the red king crab, *P. camtschatica*, and prevalence (percentage of crabs infested) and mean intensity (number of symbionts per pleopod) ($\bar{X}$ ± SD) of symbiotic nemerteans, turbellarians, and amphipods from various sites in the Kodiak Island Management area. *N* is sample size.

Management areas and collection sites	Date (mo/yr)	*N*	Crab egg mortality (%)	*C. regicides*		Nemertean form 4		Nemertean form 5		Turbellaria spp.		*Ischyrocerus* sp.	
				Prevalence (%)	Intensity ($\bar{X}$ ± SD)	Prevalence (%)	Intensity ($\bar{X}$ ± SD)	Prevalence (%)	Intensity ($\bar{X}$ ± SD)	Prevalence (%)	Intensity ($\bar{X}$ ± SD)	Prevalence (%)	Intensity ($\bar{X}$ ± SD)
Alitak Bay (AB)	2/84	15	4.4 ± 3.3	80	9 ± 5	67	16 ± 19	7	2	80	61 ± 133	47	1 ± 1
	8/84	7	1.9 ± 1.9	100	23 ± 40	71	5 ± 7	14	1	100	356 ± 407	29	2 ± 1
	2/85	13	23.7 ± 27.6	85	50 ± 28	0	—	0	—	62	46 ± 49	38	4 ± 5
	4/85[a]	15	—[b]	62	16 ± 19	40	19 ± 16	0	—	53	674 ± 954	27	7 ± 9
	4/85[a]	3	1.9 ± 3.1	0	—	0	—	0	—	33	54	0	—
Chiniak Bay (CB)	9/83	4	0.7 ± 1.3	100	5 ± 3	100	2 ± 1	25	1	100	458 ± 266	25	1
	1/84	6	0.3 ± 0.7[c,d]	33	1 ± 0	17	2	0	—	100	493 ± 371	100	2 ± 1
	8/84	5	0.3 ± 0.2	80	4 ± 4	20	2	0	—	100	166 ± 84	0	—
Chiniak Gully (CG)	8/83	10	7.9 ± 19.1	100	529 ± 550	0	—	0	—	0	—	0	—
	4/84	3	—[b]	100	41 ± 32	0	—	0	—	0	—	0	—
East of Chirikof I. (CE)	7/84	9	0.1 ± 0.1	22	2 ± 1	22	2 ± 1	0	—	100	469 ± 431	44	2 ± 1
West of Chirikof I. (CW)	7/83	3	0.0 ± 0.0	33	1	10	1	0	—	100	259 ± 237	67	2
Geese Island (GI)	2/85	8	52.6 ± 37.6[c]	75	87 ± 102	0	—	0	—	12	9	50	8 ± 6
Cape Ikolik (IK)	2/84	17	2.5 ± 1.4[c]	65	11 ± 8	82	8 ± 4	47	10 ± 7	82	469 ± 515	100	2 ± 1
	8/84	10	3.5 ± 4.4	100	5 ± 7	50	5 ± 3	0	—	100	152 ± 155	50	1 ± 0
Kiliuda Bay (KB)	2–3/83	10	—[b]	30	385 ± 288	70	48 ± 55	0	—	0	—	10	9
	2/84	12	29.5 ± 28.7[c]	92	10 ± 6	83	17 ± 9	17	2 ± 1	83	567 ± 1044	100	12 ± 17
	7/84	10	17.0 ± 14.8	100	632 ± 570	100	723 ± 871	10	2	50	169 ± 218	0	—
Sitkalidak Strait (SS)	8/83	1	70.2	100	2 024	0	—	0	—	100	5	0	—
	2/84	8	34.8 ± 32.3[c]	62	4 ± 4	50	9 ± 8	12	1	25	4 ± 3	88	18 ± 25
	6/84	10	11.3 ± 28.6	100	8098 ± 16 352	60	357 ± 350	60	2 ± 2	0	—	0	—
Terror Bay (TB)	6/84	13	72.5 ± 24.0	100	85 244 ± 22 918	100	24 672 ± 28 325	0	—	0	—	0	—
	2/85	1	100.0	100	28	0	—	0	—	0	—	0	—
Uganik Bay (UB)	9/83	5	70.7 ± 44.3	100	379 ± 309	0	—	0	—	0	—	40	1
	6/84	12	41.0 ± 19.9	100	24 935 ± 7456	100	17 654 ± 10 160	0	—	0	—	0	—
	8/84	13	84.5 ± 21.9	100	28 759 ± 29 817	100	21 952 ± 12 061	0	—	0	—	46	1 ± 1
Viekoda Bay (VB)	9/83	2	34.4 ± 48.6	100	19 ± 12	100	222 ± 37	0	—	100	93 ± 130	100	6 ± 1
	6/84	10	5.8 ± 6.9	100	1758 ± 963	100	1684 ± 978	0	—	0	—	40	1 ± 0
	8/84	5	68.4 ± 26.3	100	1415 ± 1221	100	8545 ± 8700	0	—	0	—	40	1 ± 0

[a]At AB in 4/85, 15 crabs had very late embryos from the 1983–84 brooding season and three crabs had recently oviposited early embryos from the 1985–86 brooding season.
[b]Egg mortality could not be quantified because eggs had begun to hatch in these samples.
[c]Eggs of some or all of the samples had numerous frayed funiculi consistent with heavy predation by *Ischyrocerus*.
[d]Does not include one sample with 100% egg loss and many frayed funiculi.

1 and 2). Losses were considerable (>30%) or severe (>70%) in some samples from Kachemak Bay in the Cook Inlet Management Area, Excursion Inlet and Port Frederick in the Southeastern Alaska Management Area, and at Dutch Harbor. In the Kodiak Archipelago, considerable or severe egg mortality was seen at Geese Island, Sitkalidak Strait, Terror Bay, Uganik Bay, and Viekoda Bay. Other locations exhibited little egg mortality (<5%), for example Barlow Cove in Southeastern Alaska, Kamishak Bay in Cook Inlet, and Chiniak Bay on Kodiak Island, Brood mortality was also negligible in samples from Bristol Bay and Norton Sound. In the Adak Management Area, 6.1% egg mortality was recorded.

Presence of Symbionts

Several kinds of symbionts were associated with the eggs of red king crabs. At least five species of nemerteans, one species of turbellarian, and one species of amphipod, *Ischyrocerus* sp., some of which were similar to *I. anguipes*, Sars 1895, were recognized. One species of nemertean, *C. regicides*, Shields et al. 1989, was most abundant and widespread. It is a small (1–3 mm) two-eyed nemertean and was formerly designated from No. 1 by Wickham and Kuris (1988). Four other species of symbiotic nemerteans found in these samples have been partially described (Wickham and Kuris 1988; Gibson et al. 1990). These undescribed nemertean species have been designated form Nos. 2–5 (Wickham and Kuris 1988). Form 4 is also abundant and widespread.

Carcinonemertes regicides was not present on the male and nonovigerous crabs examined. Two of these crabs were infested with juvenile worms of form 4.

Geographic Range and Abundance of Symbionts

Carcinonemertes regicides was recorded from all management areas sampled except the Alaska Peninsula, Bristol Bay,

and Adak (Tables 1 and 2). It reached very high mean intensities ($>10^3$ worms per pleopod) in Kachemak Bay (Cook Inlet), in the vicinity of Kodiak Island near Dutch Harbor, and in Southeastern Alaska (Fig. 1). It was recovered as far north as Norton Sound and as far west as Dutch Harbor. In the Kodiak Island area, where sufficient samples are available for a finer scale geographic analysis, *C. regicides* reached peak mean intensities of $>10^3$ worms per pleopod along the northwest coast of Kodiak Island and in Sitkalidak Strait.

From 4 of Wickham and Kuris (1988), a small, eyeless species, was recovered from 10 of the 12 localities in the Kodiak Archipelago, in Southeastern Alaska, along the southern coast of the Alaska Peninsula, near Dutch Harbor, and Adak (Tables 1 and 2). It was also observed in unquantified samples from Resurrection Bay, Cook Inlet Management Area. Form 4 was recovered in relatively low numbers except at Kiliuda Bay, Sitkalidak Strait, Uganik Bay, and Viekoda Bay near Kodiak Island, at some Southeastern Alaska localities, and near Dutch Harbor. At these localities, intensity was high, ranging from 10^2 to 10^4 worms per pleopod (Table 2).

Form 5 of Wickham and Kuris (1988) was also eyeless but long and robust. It was found at 5 of the 12 localities in the Kodiak Island Management Area but was never common (Table 2). Prevalence did not exceed 60% and intensity was never more than 10 worms per pleopod. It was present in Southeastern Alaska, ranged as far west as the Adak Management Area, and was found near Dutch Harbor (Table 1). However, it was absent from the several localities sampled along the Alaskan Peninsula. It was also absent from Cook Inlet, Bristol Bay, and Norton Sound. In the Kodiak Island Management Area it always cooccurred with form 4. However, in Southeastern Alaska and Adak it was generally present at localities where form 4 was absent or rare. Intensity of these worms was highest at Adak where it reached an intensity of 62 worms per pleopod (Table 1).

Form 2 of Wickham and Kuris (1988) could be recognized in fresh samples on the basis of proboscis armature measurements and the type of sheath produced by adult males. In preserved samples it was distinguished from *C. regicides* on the basis of its larger size. Examination of the size distribution of worms in our preserved samples suggests that it was not abundant at any locality. Form 2 probably includes the newly described species of symbiotic nemertean, *Alaxinus oclairi*, collected near Juneau in Southeastern Alaska (Gibson et al. 1990).

The remaining species, form 3 of Wickham and Kuris (1988), had two eyes and an expanded head. Only a single specimen was recognized in a fresh sample from Kiliuda Bay, east of Kodiak Island.

Turbellarians were widespread, ranging from Dutch Harbor in the south and west to Norton Sound in the north and Southeastern Alaska in the east (Table 1; Fig. 2). At many localities, prevalance was 100%. They reached high levels of intensity ($>10^2$ per pleopod) near Dutch Harbor, at several sites in Southeastern Alaska, and in 1 of 13 samples from Kachemak Bay. Turbellarians were recovered from 9 of the 12 localities in the Kodiak Archipelago (Table 2; Fig. 2). They reached high intensities ($>10^2$ per pleopod) at Alitak Bay, Chiniak Bay, Chirikof Island, Cape Ikolik, and Kiliuda Bay. In contrast, turbellarians were not recovered from Chiniak Gully, Terror Bay, and Uganik Bay.

Both presence and abundance of the amphipod *Ischyrocerus* sp. were undoubtedly underestimated, as these may become dislodged during collection and preservation of the samples. It was recorded as present in samples from Southeastern Alaska, west to Dutch Harbor, and north to Bristol Bay and Cook Inlet (Table 1). These amphipods were collected from 10 of 12 locations in the Kodiak Management Area (Table 2). It was absent in samples from the Alaska Peninsula and Norton Sound. When present, prevalence was generally low (often about 10%) (Tables 1 and 2). The highest mean intensities were observed in the 2/83 sample from Kachemak Bay (19 amphipods per pleopod) and the 2/84 sample from Sitkalidak Strait (18 amphipods per pleopod).

Seasonal and Annual Patterns

Our most extensive series of observations at one locality was for Kachemak Bay, south of Homer on the Kenai Peninsula. Virtually all nemerteans recovered from this area were *C. regicides* (Table 1). Shortly after oviposition in March or April, few female red king crabs were infested with nemerteans and worm intensity was very low. By June, all of the crabs examined were infested but intensity remained low. Little egg mortality was observed. Intensity rose sharply in July and August, reaching a mean approaching 2600 worms per pleopod in August 1983. Worms were readily visible in the egg mass of such heavily infested crabs. Brood mortality was appreciable in 1983 and 1984 (45–85%). In September and October, worm prevalence and intensity remained high and clutch losses rose from 59 to near 100% in those years. In the late fall and winter, nemertean intensity declined, although prevalence remained high. Egg mortality did not increase further through the remainder of the brooding period.

In Kachemak Bay, samples from the 1983–84 and 1984–85 brooding seasons exhibited mean intensities of nemerteans of 2700 and 1200 worms per pleopod, and mortality peaked at 96 and 59%, respectively. In the 1983–84 brooding season, clutch mortality was virtually total. Intensity of the infestation and the associated egg mortality subsided in the 1985–86 brooding season.

Comparable longitudinal data for the turbellarians at Kachemak Bay are lacking because only a few turbellarians were collected in but a single sample. To develop a picture of seasonal dynamics of the turbellarian, all collections from the Kodiak region were combined. Only 5 mo were represented. No consistent seasonal or annual patterns were evident.

At Kachemak Bay, the amphipod *Ischyrocerus* sp. appeared to have a seasonal pattern of abundance (Table 1). It was not recovered in any of the samples taken in the first half of the brooding season (April to August) but was present in seven of eight samples from the latter part of the brooding season (September to April). It reached its peak in both prevalence and intensity in February. These sparse observations are supported by data from other locations. From various sites in the Kodiak Archipelago, presence of the amphipod increased from 7 of the 13 samples taken early in the brooding season to 11 of 13 samples from late in the brooding season. Both prevalence and intensity were generally higher in the later samples.

Egg Loss in Captive Crabs

We compared changes in egg survival and nemertean density on crabs held in flowing seawater. At capture, the uninfested control crabs (from Kamishak Bay) had experienced negligible egg mortality (2.4%) which did not increase during the 120 d of captivity (Fig. 3). In contrast, crabs from Kiliuda Bay had

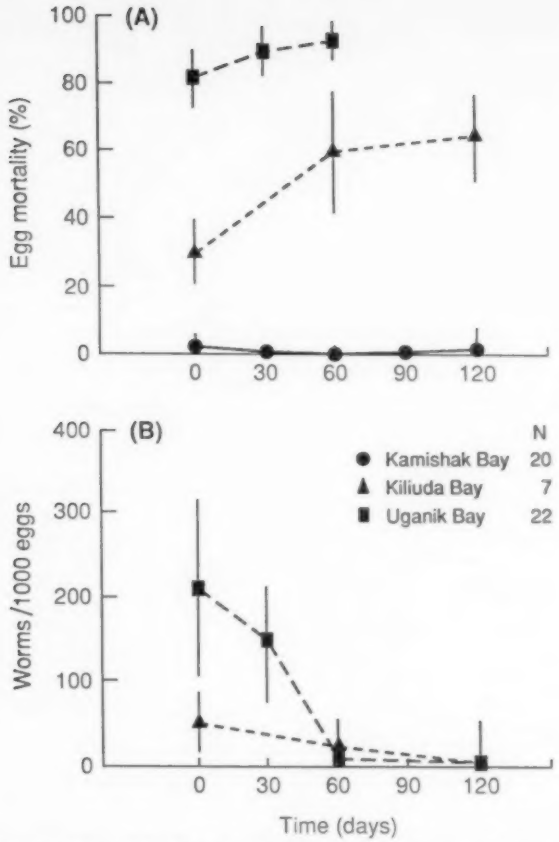

FIG. 3. Changes in (A) egg mortality and (B) nemertean density (worms per 1000 crab eggs) of *C. regicides* on red king crabs held in captivity for 120 d at the Seward Marine Center. Clutches were from the 1985–86 brooding season. Uninfested control crabs were collected from Kamishak Bay, Cook Inlet. Infested crabs were collected from Uganik and Kiliuda bays, Kodiak Island, Alaska. Error bars represent standard deviations.

an initial mortality of 30% and a mean density of 48 nemerteans per 1000 crab eggs. Mortality rose to 68% over the 120-d observation period. Nemertean abundance decreased substantially over the observation period. Crabs from Uganik Bay had already suffered 86% egg mortality upon capture. Over 60 d, mortality increased to 94%. Nemertean abundance of these crabs was 204 per 1000 crab eggs at the start and declined to 3 per 1000 crab eggs at the end of the observation period. A comparable loss of nemerteans in situ under captive conditions has also been observed for *Carcinonemertes epialti* on *Hemigrapsus oregonensis* (Kuris 1978).

Feeding Behavior of Symbionts

Examination of living worms from captive crabs revealed that most worms were *C. regicides*. Some of the small eyeless nemerteans (form 4) were present. Both species of nemerteans were observed feeding on crab eggs in vitro. These nemerteans were seen to pierce intact egg membranes and feed on the contents using the sucking action of their pharynx as reported for other species of *Carcinonemertes* (Wickham 1978; Roe 1984). In addition, crab egg yolk and eye placodes were frequently observed in the gut of both species of nemertean worms removed from crab egg masses.

Turbellarians, although sometimes quite numerous, were not observed to feed on intact eggs. However, in vitro observations indicated that they did move in the direction of a ruptured egg and fed on the contents.

Dissections of the amphipod *Ischyrocerus* sp. revealed numerous crab egg membranes packed in the gut. When feeding, these amphipods apparently detached the eggs from the funiculi. In a few samples from the Kodiak Archipelago, frayed funiculi, indicating detachment of eggs, were often observed and could be counted (Table 2). Three of these four sites had substantial egg mortality (29–53%) and had the three highest intensities of amphipods reported from the Kodiak Island Management Area (8–18 amphipods per pleopod).

TABLE 3. Pearson product-moment correlation (r) for egg mortality (%) in relation to intensity of various symbionts inhabiting the clutch of *P. camtschatica*. Data from crabs collected in the Kodiak Island Management Area from June to August 1984 ($N = 80$). *$0.01 < P < 0.05$, **$P < 0.01$, correlation coefficients significantly different from zero.

Symbiont	r
Carcinonemertes regicides	0.552**
Nemertean form 4	0.458**
Both nemerteans[a]	0.657**
Turbellarians	−0.326*
Ischyrocerus sp.	0.010

[a]*C. regicides* and nemertean form 4 combined for analysis.

TABLE 4. Correlation (r) matrix for the various symbionts found in the clutches of *P. camtschatica*. ND indicates comparison was not made. Data are from crabs collected in the Kodiak Island Management Area from June to August 1984 ($N = 80$). *$P < 0.05$, correlation coefficient significantly different from zero.

	C. regicides	Nemertean form 4	Turbellaria
C. regicides	—		
Nemertean form 4	0.138	—	
Both nemerteans[a]	ND	ND	−0.264*
Turbellaria	−0.180	−0.218*	—
Ischyrocerus sp.	−0.031	0.025	0.115

[a]*C. regicides* and nemertean form 4 combined for analysis.

Association of Egg Mortality with Symbionts

Collections from the Kodiak Island Management Area during June to August 1984 ($N = 80$) were used to analyze the relationship between egg mortality and symbiont infestation. In these samples, most of the symbionts were found at relatively high intensities and sufficient time had elapsed for brood mortality to be evident. Egg mortality was strongly correlated ($P < 0.01$) with the intensity of *C. regicides* infestations, the intensity of nemertean form 4 infestations, and the intensity of both nemertean infestations combined (Table 3). The intensity of the turbellarian infestations was negatively correlated with egg mortality, while that of amphipod infestations was not correlated with egg mortality.

The intensity of the turbellarian infestations was significantly negatively correlated with intensity of both *C. regicides* and form 4 combined (Table 4). Intensity of *C. regicides* was not correlated with intensity of form 4, and intensity of neither the

nemerteans nor turbellarians was correlated with the amphipod (Table 4). Similar trends were noted from other collection sites and when all of the samples were combined for analysis.

Seasonal variation in the correlation of egg mortality of *P. camtschatica* with intensity of *C. regicides* infestations was examined at Kachemak Bay, as other symbionts were rare or absent at this location. Here, infestation by *C. regicides* was strongly correlated with egg mortality during July ($r = 0.814$, $P < 0.01$) and February ($r = 0.906$, $P < 0.001$). Egg mortality was also highly correlated with intensity of *C. regicides* when all the monthly samples were combined ($r = 0.548$, $P < 0.001$).

Discussion

This survey documents high mortality of red king crab embryos from 1983 to 1985 at certain locations in Alaska. Several consistent features were associated with egg mortality. Sites exhibiting high mortality were geographically clustered, notably in the Kodiak Archipelago and Southeastern Alaska. Further, impacted areas were usually affected in all of the brooding seasons for which data were available. Two features are consistently associated with substantial brood losses. Firstly, high egg mortality usually occurred when high-intensity infestations of symbiotic nemerteans were recorded in the egg mass. Secondly, mortality, where it occurred, was strongly seasonal.

Certain broad geographic regions experienced negligible (<5%) egg mortality. These included the Alaska Peninsula, Bristol Bay, and Norton Sound. Some locations were uninfested although they were within the same management area as were locations experiencing severe egg mortality. For example, Kachemak Bay was severely impacted, while across Cook Inlet, Kamishak Bay was unaffected. Variation in the extent of egg mortality was also considerable in the Kodiak Archipelago.

Generally, locations that were in close proximity had similar patterns of egg mortality, nemertean species composition, and intensities. For example, Excursion Inlet and Port Frederick in Southeastern Alaska face each other across the 25-km-wide Icy Strait. At both sites, mortality was substantial and infestation patterns were similar, with intensities of $>10^4$ *C. regicides*, $>10^3$ form 4, and no form 5. In contrast, Gambier and Pybus coves, whose entrances are separated by 20 km, had low egg mortality, had few *C. regicides*, lacked form 4, and had similar low intensity infestations of form 5. Similarly, in the Kodiak Archipelago, Uganik, Viekoda, and Terror bays are in close proximity and had very high egg mortality and comparable high-intensity nemertean infestations ($>10^4$). Locations east and west of Chirikof Island had low egg mortality and comparable low-intensity infestations of nemerteans.

In situ and in vitro laboratory observations and the presence of crab embryo fragments in the gut of the nemerteans demonstrated that egg predation by the symbionts was the cause of most of the observed egg mortality. This was supported by the data on distribution and abundance of the worms. Either *C. regicides* or form 4 were absent or rare in almost all samples when egg mortality was less than 5% and were present in abundance in almost all samples having more than 10% egg mortality.

Our study probably underestimated egg mortality of red king crabs, since mortality estimates were based on the proportional loss of eggs from samples mostly obtained 3–6 mo into an 11-mo brooding season. Thus, we do not consider the likely continued loss of eggs to brood predators during the remainder of the season. To project these losses for an estimate of total mortality through the entire brooding season, as has been calculated for the shore crab *Hemigrapsus oregonensis* (Shields and Kuris 1988a), estimates of feeding rates and the duration of the feeding period would be necessary. This information is not available for the egg predators of red king crab. Both direct in vitro observations on individual worms (Roe 1984; Okazaki 1986; Shields and Kuris 1988b) and indirect methods (Kuris and Wickham 1987) are available for estimation of nemertean feeding rates.

The cause of the outbreak of symbionts to epidemic levels is unknown, as is the reason for its apparent subsidence. It is also difficult to place this in a historic perspective, as detailed examinations of red king crab egg clutches for symbionts have not been a regular feature of stock monitoring policy. Presumably, *C. regicides* and the other nemertean symbionts have coexisted with king crabs. What appears to be unusual, perhaps unique, is the outbreak from low endemic levels to the epidemic levels documented here. One might expect that the high-intensity infestations would have been observed and reported from relatively accessible and well-studied stocks such as those near Kodiak Island and Cook Inlet. However, Haynes (1986 *in litt.*) recalled that "*Carcinonemertes* were not uncommon" in Kachimak Bay in the 1960's. This suggests that at certain locations, annual nemertean outbreaks, resulting in significant brood losses, may often occur but have been unrecognized or unreported.

Substantial reduction in clutch sizes and complete loss of clutches have been noted to affect specific stocks in the past (Powell and Lebida 1968; McMullen 1968). In the 1960's, adult female red king crabs from several stocks in the Kodiak Island Management Area did not carry eggs or sloughed their eggs in the first half of the brooding season. Affected females were infertile, as they either never oviposited (resorbing their ova), or their extruded eggs never embryonated (McMullen and Yoshihara 1969). Overfishing of male crabs was suggested as the cause of the insufficient fertilization rate (McMullen 1968). Our observations indicate that egg predation by symbiotic nemerteans can also be an important source of brood failure. Infertility and egg predation can be distinguished by the timing of brood loss as well as by direct observations on the egg mass and ovary. It would be useful to examine whether stocks with heavy infestations of nemertean egg predators experienced greater fishing pressure than did similar stocks with low-intensity infestations.

Blau (1986) observed that poor recruitment of juvenile red king crab began as early as 1978 in the Kodiak Island Management Area. We cannot, at present, evaluate whether nemertean egg predation contributed to the onset of poor area-wide recruitment, but it may impact recruitment in some local areas. It is probable that the epidemic levels of nemertean egg predators will exacerbate recovery of certain stocks. As there is an 8- to 10-yr lag between spawning and recruitment to legal size (Blau 1986), the effects of the 1983-85 episode of brood failure should be most evident in 1991–93. The importance of these effects will be strongly dependent on transport patterns of larvae and resultant patterns of early recruitment. The geographic variation in productivity, seen in the episodes of brood failure in both the 1960's and 1980's, supports the need for further studies of larval transport and settlement (Incze 1985; Jamieson 1986).

Our survey recovered and quantified an unsuspected diversity of symbionts in the egg masses of the red king crab. In the

samples from the Kodiak Archipelago, *C. regicides* often cooccurred with nemerteans forms 4 and 5 (Table 2). Elsewhere, however, this pattern of cooccurrence was not evident (Table 1). Most notably, at Kachemak Bay, *C. regicides* was very abundant and was the only nemertean present in the numerous samples available at this locality. Adak appeared to be the only locality where a nemertean other than *C. regicides* or form 4 was the principal cause of egg mortality.

The turbellarians appear to be harmless commensals. Their primary source of food is unknown. They may obtain some nutrition by feeding on the remnants of eggs after nemertean predation. This could be an important food source, as small nemerteans consume only a small portion of the egg contents (Roe 1984). Also, the negative association of the turbellarians with the nemerteans suggests the possibility that the turbellarians may be predators on the nemerteans.

Species of *Ischyrocerus* have not previously been reported as crustacean egg predators. These amphipods are probably not sufficiently abundant to often have a significant impact on productivity of the red king crab. However, the association of high amphipod intensities with numerous frayed funiculi and substantially reduced clutch sizes at a few locations near Kodiak Island suggests that these symbiotic amphipods may occasionally have a significant negative effect on egg output.

The locations where nemerteans were most abundant are all narrow fjords, inlets, or passages, often with shallow sills. For example, Terror Bay has two sills as does the head of Uganik Bay. Locations with a low mean intensity of nemerteans include a variety of oceanographic and topographic conditions such as oceanic banks, open coasts, embayments, and fjords. The distribution of these nemerteans elsewhere in Alaska is consistent with this pattern. In Southeastern Alaska, high mean intensities of nemerteans were recorded from fjords and inlets such as Excursion Inlet and Port Frederick (Table 1) which have sills at their entrance. In Cook Inlet, Kamishak Bay, where crabs were lightly infested, is a shallow, open embayment whereas Kachemak Bay, where heavy infestations were documented in all years, is partially enclosed by a spit at Homer and a low sill.

Sloan (1984) has proposed that fjords, particularly those with shallow sills, may entrap rhizocephalan larvae and that retention of larval parasites may contribute to their persistent high prevalence and intensity at such locations. This sort of environment may also contribute to the establishment of nemertean outbreaks and their persistence at high intensities.

In contrast, high intensities of turbellarians were generally found at locations other than narrow fjords, inlets, and passages. In the Kodiak Archipelago, mean turbellarian intensities $>10^2$ worms per pleopod were recorded from very open sites such as Cape Ikolik, the east and west coasts of Chirikof Island, and from open embayments or fjords such as Chiniak, Alitak, and Kiliuda bays. Elsewhere in Alaska, high intensities of turbellarians were noted in collections from some of the fjords and passages of Southeastern Alaska and the open coast near Dutch Harbor. In contrast with the nemerteans, turbellarians were commonly recovered from the Bering Sea localities. These observations suggest that the mechanisms of recruitment for the nemertean and turbellarian symbionts are quite different.

At Adak and four of the six Southeastern Alaska locations, the species composition of the nemertean guild differed from the remaining areas. At these sites, a large nemertean, form 5, was either the most abundant nemertean or matched the order of magnitude of *C. regicides* infestations. Further efforts devoted to the systematics of these nemerteans should be focused on Adak and Southeastern Alaska.

The natural history of *C. regicides* on *P. camtschatica* reveals some of the epidemiological features of this host–symbiont system that may have contributed to the outbreak. Very low prevalence and intensity early in the brooding season (March to May) suggests that few worms are retained on females during the brief interbrood period; nor are worms transmitted from males to females during copulation, as experimentally shown for *C. errans* on Dungeness crabs (Wickham et al. 1984). In June, the worms spread through the entire host population and intensity begins to rise. Through June there is little egg mortality and worm intensity and egg mortality are not correlated. In July and August, worm intensity surges to high levels of over 2000 worms per pleopod and intensity and egg mortality are highly correlated. As high worm numbers persist through September and October, most of the eggs are eaten. Worm intensity decreases markedly late in the brooding season (November to February), but all crabs remain infested.

This temporal pattern suggests that the duration of the transmissive larval stage for *C. regicides* is brief and that crabs are rapidly and continually reinfested by larvae that have dispersed but a short distance in the plankton. An abbreviated life cycle, perhaps incorporating autoinfection, would account for the very rapid increase in nemertean intensity, over three orders of magnitude, seen over a few months in samples from Kachemak Bay (Table 1). Such a life cycle would be particularly damaging to host populations in the enclosed fjords and passages where *C. regicides* reached peak intensities. Direct development, with an ephemeral nonplanktonic larva, has been described for *Pseudocarcinonemertes homari* in the American lobster, *Homarus americanus* (Aiken et al. 1985). Indeed, autoinfection has been documented for *P. homari* on lobsters (Aiken et al. 1985).

The rapid increases in intensity seen for *C. regicides* during a brooding period have not been observed in other nemertean–host associations. Instead, small but significant changes in nemertean intensity during a brooding period have been noted in these systems (Kuris 1978; Brattey et al. 1985; Shields et al. 1990a).

In contrast with *C. regicides* on *P. camtschatica*, juvenile *C. epialti*, *C. errans*, and form 4 are regularly found in abundance on the exoskeletons of male and nonovigerous female hosts (Kuris 1978; Wickham et al. 1984; A. M. Kuris and D. E. Wickham, unpubl. obs.). In these other systems, effective transmission between instars at molt, and from males to females at copulation, delivers large numbers of worms to the ovipositing female (Wickham et al. 1984).

For other nemertean egg predators, increased rates of egg mortality during the brooding season are attributed primarily to increased growth and feeding of the adult worms (Kuris 1978; Kuris and Wickham 1987; Shields and Kuris 1988a; Shields et al. 1990a). In contrast, *C. regicides*, the smallest known adult nemertean egg predator, produces increased egg mortality by a numerical response rather than by a developmental (growth) response.

For *C. errans* on *C. magister*, prevalence of nemerteans was 80–100% even in lightly infested populations (Wickham 1986). Efficiency of transmission of juvenile worms may have stabilized population levels and decreased the degree of aggregation of worms on hosts. Where outbreaks occurred, such as for *Carcinonemertes epialti* on *H. oregonensis*, even male and nonovigerous female crabs exhibited high-intensity infestations (Shields and Kuris 1988a). Delivery of these worms to the ovi-

gerous females may have contributed to the high-intensity infestations seen on females with recently oviposited broods. In contrast, *C. regicides* appears able to undergo a population explosion on ovigerous red king crabs, relying on transmission solely between ovigerous females. Reliance on larval transmission, perhaps involving competent larvae that settle on crabs after a very brief planktonic existence, may be an important adaptation facilitating the localized outbreaks of epidemic proportions seen on the red king crabs in Alaska.

The spatial and temporal patterns of nemertean abundance documented here do not implicate the fishery as a contributor to the pervasive brood failure seen in some stocks of red king crab. However, the reproductive output of several localized areas has been greatly reduced due to nemertean egg predation. Additional monitoring of crab reproduction would facilitate retrospective studies of crab fecundity, expand our knowledge of the systematics and ecology of clutch symbionts, and may permit development of more precise fishery closure standards. A baseline for assessment of future reproductive crashes would provide continued perspective on the past and might guide management decisions in the future.

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Density-Dependent Maturation, Growth, and Female Dominance in Lake Superior Lake Herring (*Coregonus artedii*)

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Density-related changes in age at maturation, sex ratio of recruits, growth, and fecundity at very low density result in spawning populations which comprise many older females and few young males and in which egg production per lake herring (*Coregonus artedii*) is increased by a factor of five. Age of maturation is delayed at low density for females, but not for males. Thus, males dominate the youngest age classes but females become increasingly more abundant from age 2+ through age 6+. A model of lake herring population structure showed that although delayed maturation accounts for many characteristics of depressed populations, it does not explain overall population femaleness. The model was used to evaluate effects of differential adult mortality, recruitment failure, and changes in the sex ratio of recruits, and only the latter provided an adequate explanation for overall femaleness. Despite the apparently compensatory nature of these responses, the slow and unsteady recovery of depressed Lake Superior populations during the last two decades indicates that one or more additional factors play important roles in determination of year class strength.

Des variations, liées à une très faible densité, de l'âge à la maturité, de la proportion relative des sexes des recrues et des taux de croissance et de fécondité donnent lieu à des populations génitrices composées d'un grand nombre de femelles âgées et d'un faible nombre de jeunes mâles ainsi qu'à une production quintuplée d'oeufs par cisco de lac (*Coregonus artedii*). À de faibles densités, la maturité est retardée chez les femelles, mais non chez les mâles. Ainsi, les mâles sont les plus abondants dans les jeunes classes d'âges, mais le nombre de femelles augmente progressivement à partir de la classe 2+ jusqu'à 6+. Un modèle de la structure démographique du cisco de lac révèle que même si la maturité retardée explique un grand nombre des caractéristiques des populations inférieures à la normale, elle n'explique pas le caractère femelle de la population. On a utilisé le modèle pour évaluer les incidences d'un taux différentiel de mortalité des adultes, la faillite du recrutement et les variations de la proportion relative des sexes des recrues. Seule cette dernière variable fournit une explication adéquate du caractère femelle global. Malgré la nature apparemment compensatrice de ces réactions, le lent rétablissement instable des populations inférieures à la normale du lac Supérieur au cours des deux dernières décennies révèle qu'un autre facteur, ou plus d'un, joue des rôles importants dans la détermination de l'abondance des classes d'âges.

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For nearly a century, lake herring (*Coregonus artedii*) was the most productive species in the Lake Superior fishery. Catch statistics for the period 1935–60 show that the lake herring fishery produced an average of 75% by weight of the fish harvested from American waters of the lake (NOAA 1960). But beginning in the early 1960's, lake herring catches declined dramatically, and by 1970, many populations were reduced to < 1% of pre-1950 levels (Selgeby 1982). Although exploitation in most American waters ceased by 1970, depressed populations generally did not rebound as expected and some continued to decline well into the mid-1970's even in the absence of a fishery.

With a sense of some urgency, the Great Lakes Fishery Commission convened in 1972 a special Lake Herring Subcommittee with the charge to evaluate the status of Lake Superior populations and to recommend management alternatives and research priorities that would contribute to the resource's rehabilitation. In its summary report, the Subcommittee identified two little-understood characteristics of collapsed, nonrecovering populations (Wright 1972). First, fish that made up the spawning populations showed an increased mean age. Whereas stable, higher density populations have a mean age of approximately 3.8 yr, collapsed populations typically ranged in mean age from 5 to 7 yr. Second, whereas spawners in higher density, stable populations exhibit a 50:50 sex ratio, collapsed populations ranged from 35 to 90% females. Populations dominated by females were more common.

The research reported here was initiated at the request of the Michigan Department of Natural Resources who was concerned

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that departure from a 50:50 sex ratio may have been an impediment to population recovery.

Methods

Our approach was to characterize three remaining lake herring populations in Lake Superior in the early 1980's and compare these with earlier populations in Lake Superior and elsewhere. We determined population structure, mortality rate, maturation, and size at age for lake herring that gather to spawn in (1) waters north of Marquette, Michigan, (2) south and east of the Keweenaw Peninsula, Michigan, and (3) east of Duluth, Minnesota. Fecundity was examined for only the Keweenaw population. Data from our own collections made from 1980 to 1983 when these populations were variously depressed were compared with data for heavily exploited and declining lake herring from the same areas of Lake Superior studied prior to population collapse from 1950 to 1962 by Dryer and Beil (1964), with the moderately exploited, stable lake herring population at Bay City, Lake Huron, studied from 1921 to 1924 by Van Oosten (1929), and with several populations in smaller lakes. Using a population age structure and sex ratio model, we evaluated various life history variables and population processes to identify those most likely to be responsible for characteristics particular to low-density populations. From these results, we inferred the significance of population age structure and sex ratio at low density for population recovery.

Collections were made at intervals of a few days during the spawning season (November–December) at depths of 50–145 m with 6.6-cm (2 5/8 in.) and 6.9-cm (2 3/4 in.) stretch measure, multifilament gill nets. Gill nets were used because they are the only effective means for sampling low-density populations. Preliminary calculations in which we corrected for net selectivity by reference to relative, size-specific capture efficiencies in a six-panel, multiple-mesh gill net (Regier and Robson 1966) gave population structures similar to those reported below. In order that our data may be compared with those reported by other authors, we have not applied these corrections in data reported here.

Keweenaw waters were sampled from 1980 through 1983. Marquette and Duluth waters were sampled from 1981 through 1983 with the exception that storms prevented sampling in Marquette waters in 1983. Effort per year per area ranged from 11.5 to 81.2 km net nights. Collections were made by cooperating commercial fishermen under special permits issued by the Michigan and Minnesota Departments of Natural Resources.

A subsample of 40 lake herring per catch was retained for analysis. In catches containing fewer than 40, all those caught were analyzed. Total length (cm) (centimetres) sex, and in some cases weight (grams) were recorded. Scales were taken from the left side of the fish between the dorsal fin and lateral line. If scales were absent from this region, they were collected from the region immediately posterior. Five scales from each fish were cleaned with water and examined on a microfiche projector (36× magnification). Annual checks were distinguished from other patterns by a clear series of discontinuous circuli in both anterior and lateral fields. Age was determined by counting annual checks in the lateral field of the scale (Van Oosten 1929; Hile 1936). The number of fish for which age was determined ranged from 80 to 667 per sample area per year, with a total of 4029 such determinations.

From 25 ripe females with intact ovarian membranes collected in Keweenaw waters in 1983, all eggs were removed from the body cavity and stored in Gilson's fluid (Bagenal and Braum 1978). Fecundity (eggs per gram of body weight) was determined by air drying and weighing the whole egg mass, counting the eggs in four fractions of known weight, and dividing the total weight by the mean individual egg weight (Bagenal and Braum 1978).

Most previous work on lake herring growth is reported in terms of back-calculated length at age. In our work, this approach could not be used due to the variable occurrence of Lee's phenomenon both within and among populations (Gutreuter 1987). As an alternative, mean length at capture was compared directly for age 3+ lake herring collected during the spawning season at different sites.

Mortality as an instantaneous rate was calculated by comparing catch per effort (CPE, number of fish per kilometre of net per night) for individual year clases in successive years (Ricker 1975). This approach has the advantage of being less affected by the highly variable year class strength that is typical of lake herring populations. Because almost no lake herring fisheries remained in the areas studied, these values were taken as instantaneous rates of adult natural mortality (Za).

A model was developed to simulate the effects of changes in sex ratio at recruitment, year class strength, and maturation and mortality rates on population age structure and sex ratio. For age classes 1+ through 9+, the numbers of adults ($A_{s,t}$) and juveniles ($J_{s,t}$) of each sex (s) at age (t) were calculated as

$$J_{s,t} = (J_{s,t-1} - (J_{s,t-1} \times M_{s,t}))e^{-Z_j}$$

and

$$A_{s,t} = A_{s,t-1}e^{-Za} + J_{s,t-1}e^{-Z_j} \times M_{s,t}$$

where $M_{s,t}$ = the proportion of individuals of sex s that mature at age t, Z_j = the instantaneous rate of juvenile mortality, and e = the base of natural logarithms. Juvenile mortality was taken as 0.2 based on estimates for coregonids in Lake Michigan (Jude et al. 1978). The difficulty of quantitatively sampling juvenile lake herring at low population density prevented our confirming the accuracy of this estimate for Lake Superior. Model results to which this assumption is important are discussed below. Values of $M_{s,t}$ were chosen to simulate the structure of the stable Bay City population ($M_{m,2\ldots4} = M_{f,2\ldots4} = 0.1, 0.6, 1.0$) (Fig. 1a and 3a). The numbers of males and females in age class 0+ were set to simulate the effects of constant year class strength, declining year class strength (recruitment failure), or changes in the sex ratio of recruits to the adult population. The model population was stepped through nine simulation years so that starting conditions determined population characteristics at each age.

Results and Discussion

First we characterize population structures associated with high-density and low-density populations. Next we consider density-related changes in various life history variables as probable causes of the population structure typical of populations with very low density. Then we examine the relationship between density and two production variables, individual growth and fecundity, that affect population dynamics. Finally, we combine results for life history and production variables to consider the significance of low-density population structure for population recovery.

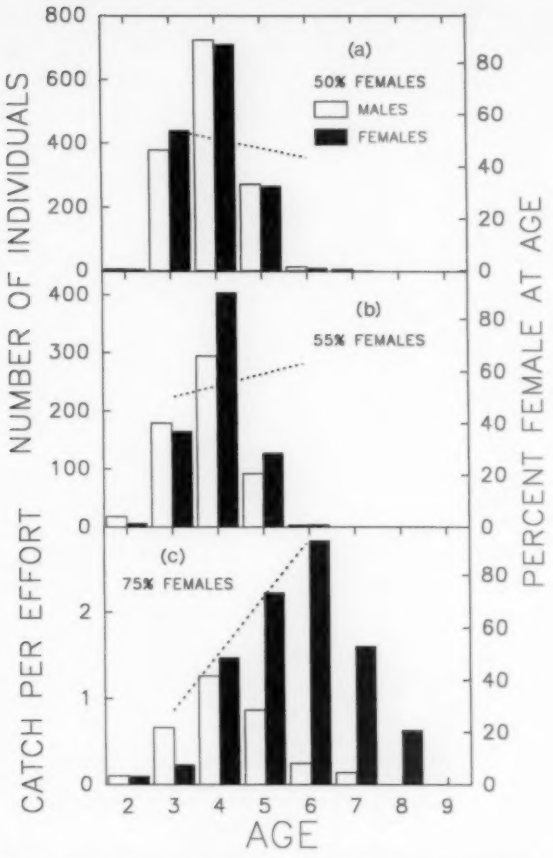

FIG. 1. Comparison of structure in three lake herring populations at different levels of exploitation. (a) The population sampled at Bay City, Lake Huron, from 1921 through 1924 by Van Oosten (1929) was moderately exploited and population numbers were stable. Modes for both sexes were age 4+ and the sex ratio is essentially 50:50 within age classes and in the population as a whole. (b) The population sampled in Keweenaw waters, Lake Superior, by Dryer and Beil (1964) during the period 1950–59 was intensively exploited and declining. A tendency toward increasing female dominance in older age classes resulted in 55% females in the population as a whole. (c) The remnant of a collapsed population at Keweenaw waters sampled in 1980 with the male mode at age 4+ and the female mode at age 6+ showed increasing female dominance with increasing age and an overall population composed of 75% females. Broken lines show linear regressions of percentage of females at age, on age (Table 2).

Population Structure in Relation to Population Density

The age and sex structure of three lake herring populations that differed in density and degree of exploitation are compared in Fig. 1. The stable population at Bay City from 1921 to 1924 showed equal numbers of males and females within each age class, both male and female modes were age 4+, and the mean age was 4.0 (Van Oosten 1929) (Fig. 1a). In contrast, the collapsed population in Keweenaw waters in 1980 comprised 25% males with a mean age of 4.3 yr and 75% females with a mean age of 5.7 yr (Fig. 1c). Mean age for the population as a whole was 5.3 yr. Whereas the male mode remained at age 4+, the female mode was age 6+. Males were more abundant than females at age 3+, but females were increasingly more abundant than males from age 4+ to 8+. Dryer and Beil (1964) reported age and sex of lake herring from Keweenaw waters pooled for the years 1950–59, a period of intense fishing effort and peak harvest that preceded the precipitous decline of the 1960's. Although both male and female modes were age 4+ and mean ages were 3.8 and 3.9, respectively, a shift toward female dominance is apparent in the older age classes resulting in a population that was 55% female (Fig. 1b).

Advanced female mode and increasing female dominance with age were consistent features of low-density populations, as seen also in the Keweenaw populations for 1981, 1982, and 1983 (Fig. 2). Data from Clady's (1966, table 22) study of Birch Lake reveal these characteristics for that population after its collapse. In the work below, we have attempted to identify relationships between population density, total population femaleness, and life history variables such as mortality, maturation, and recruitment that can account for the structure of low-density populations.

Mortality of Adult Males and Adult Females

One explanation for characteristics of low-density populations could be that adult males experience higher mortality rates than adult females at low density. Year class instantaneous mortality rates calculated separately for adult males and adult females ranged from 0.03 to 3.23, with a mean of 0.94 (Table 1). Peck (1975) found a similar range of values for both sexes combined in Keweenaw waters during the period 1961–70. In our own data, neither male nor female mortality was related to site or year of collection (ANOVA, $P > 0.20$). Thus, mortality rates for male and female year classes were paired for each collection site and year according to the number of years elapsed since their full recruitment to the adult population. A paired t-test indicated that rates for males and females were not significantly different ($P = 0.41$). At a significance level of 0.05, with $n_1 = n_2 = 14$ and using the observed pooled variance of 0.57034 to estimate the true variance, we estimate that the probability of rejecting the null hypothesis of equal means is relatively high, 0.78, if the difference is 0.8 (Montgomery 1984, p. 101). Evaluated in the population structure model, a difference of 0.8 (female $Z = 1.0$, male $Z = 1.8$) is insufficient to create a population of >50% females when differences in maturation rates are considered (Fig. 3c). Thus, differential mortality of adult males and females does not appear to be an important factor shaping spawning populations at low density. If depressed populations are increasingly dominated by females at each older age, yet males do not leave the adult population more rapidly through mortality, then perhaps females enter the adult population on a different maturation schedule than males.

Age at Maturation in Relation to Population Density

Some characteristics of low-density populations may be explained as consequences of density-dependent differences in male and female maturation. Determination of maturation schedules for lake herring presents particular problems. Especially at low density, juveniles are very difficult to sample and thus the proportions of mature and immature individuals in an age class cannot be determined directly. As an alternative, we compared the ratio of females to males at age 3+. Neither sex is fully recruited to the adult population at this age (Fig. 1). Thus, if we assume that the sex ratio of juveniles is constant (see below), the relative abundance of females at age 3+ should provide a sensitive indicator of differences in the rates of maturation of males and females.

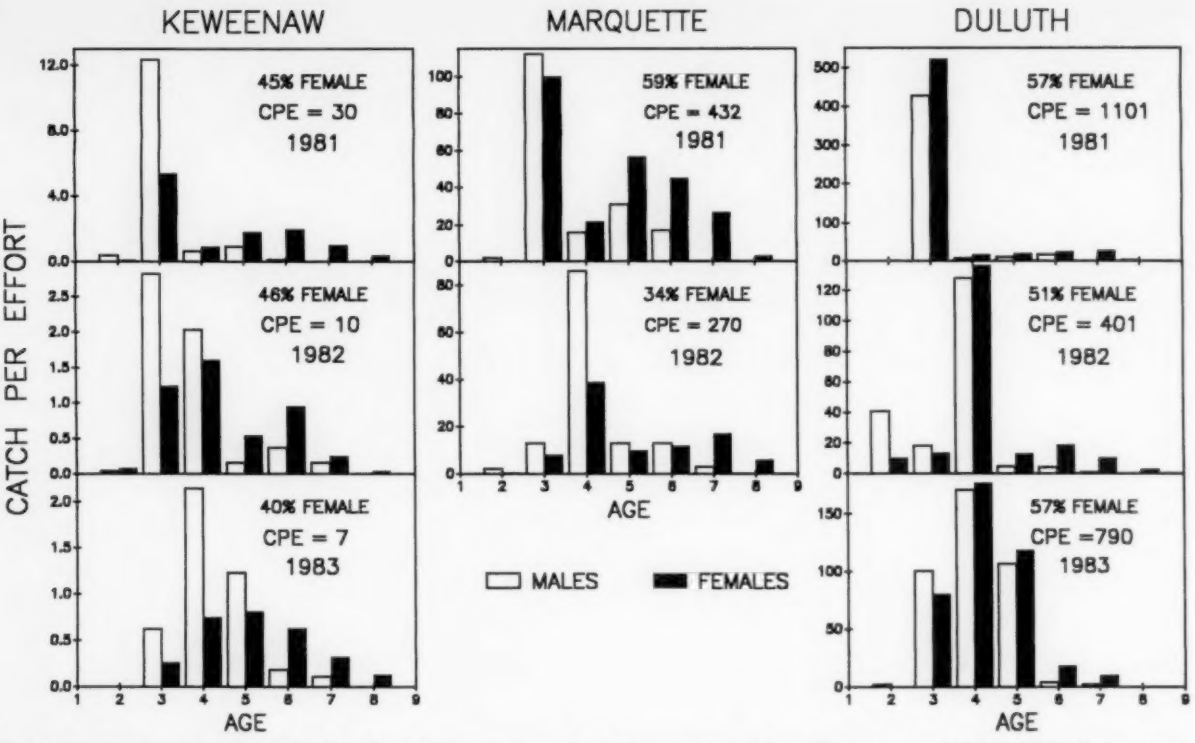

FIG. 2. Population structures for Lake Superior lake herring at very low (Keweenaw), moderate (Marquette), and higher (Duluth) densities in the early 1980's. The strong 1978 year class entered all three populations at age 3+ in 1981. By 1983, little had changed in the Keweenaw population whereas the Duluth population had attained a structure similar to that of a stable population (Fig. 1a). Despite this, none of these populations increased significantly in number until the entry of the strong 1984 year class in 1987.

Data from collections made during the present study show a strong relationship between population density and the timing of female maturation. As CPE's are compared from a high of 1200 down to 7, the sex ratio at age 3+ declines from roughly 50:50 to 30:70 (females to males) (Fig. 4). Data from the 1978 year class underscore the responsiveness of this ratio to local population density (Fig. 2). This was the first strong year class for over a decade in the American waters of Lake Superior and thus, catch rates were relatively high and CPE data can be interpreted with greater confidence. As the 1978 year class entered spawning populations at age 3+ in 1981, they were 55% female at a population CPE of 1101 in Duluth waters, 47% female at a population CPE of 212 in Marquette waters, and 34% female at a population CPE of 31 in Keweenaw waters. This could mean that at low density, males mature earlier or that females mature later. The fact that the male mode remains at age 4+ while the female mode moves from age 4+ to age 5+, 6+, or 7+ in depressed populations indicates that the change in sex ratio at age 3+ is due to delayed female maturation.

Delayed female maturation is both necessary and sufficient to create a bimodal spawning population with the female mode at an older age and with increasing female dominance from ages 1+ to 6+ as is typical of depressed populations. The population structure model shows that a shift in age at full maturity for females from 4+ to 6+ is sufficient to account for both the shift in the female mode and the degree of female dominance within age classes (Fig. 3b). Males are most abundant in the earlier age classes because they mature more rapidly, but females continue to join the adult population up to age 6+ and thus become increasingly more abundant than males with age. Delayed female maturation is necessary, since other possible explanations such as a particular sequence of sex-specific mortality rates or variable recruitment that may mimic depressed populations produce a transient population structure rather than the persistent structure characteristic of depressed populations.

Delayed female maturation does not account for overall female dominance (Fig. 3b). Other factors being equal, delayed maturation of females would result in male dominance of the spawning population, since females would be subjected to continuing mortality during the protracted juvenile phase. What then is the relationship between deferred female maturation and overall femaleness in lake herring populations?

Variation in overall femaleness is typical of lake herring in lakes throughout its range. In many populations, the degree to which female maturation is deferred cannot be reliably assessed by simple comparison of male and female modes, since year class strength is highly variable and may obscure the age of full recruitment to the adult population. This is especially true in smaller lakes. A more sensitive approach is to calculate the slope of changing female dominance at age with increasing age (Fig. 1). In populations for which this slope is zero, both sexes mature according to the same schedule. For positive slopes, the greater the slope the more female maturation is delayed relative to male maturation.

In applying this approach, we calculated slopes by least squares regression from data published for 13 lake herring populations also sampled with gill nets (Table 2). To avoid effects of extreme ages or small samples, the analysis was limited to

TABLE 1. Instantaneous mortality estimates for individual year classes of male and female lake herring in three Lake Superior spawning populations. In all populations, males were considered fully recruited at age 4+. Females were considered fully recruited at age 5+ in Marquette and Duluth waters and at age 6+ in Keweenaw waters.

Population	Sampling years	Year after full recruitment	Male Z_a	Female Z_a
Keweenaw	1980–81	1st	0.034	0.108
		2nd	0.325	1.030
		3rd	2.266	1.472
Keweenaw	1981–82	1st	1.806	0.655
		2nd	1.356	2.100
		3rd	0.900	3.229
Keweenaw	1982–83	1st	0.277	1.103
		2nd	0.482	0.638
Marquette	1981–82	1st	0.264	0.788
		2nd	0.208	1.558
		3rd	0.949	0.973
Duluth	1981–82	1st	1.206	0.276
		2nd	0.442	0.062
		3rd	0.942	0.846
Mean[a]			0.818	1.060
Median[b]			0.691	0.910

[a]Paired t-test, $P = 0.405$.

[b]Mann–Whitney pairs test, two-tailed probability of equaling or exceeding critical test statistic = 0.476.

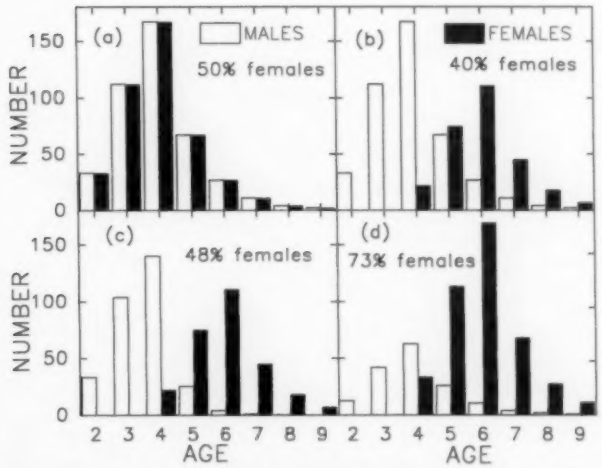

FIG. 3. Results from a model that simulates lake herring population structure. (a) Equal rates of maturation and mortality and a 50:50 sex ratio at recruitment simulate stable populations (Fig. 1a); (b) female maturation delayed for 2 yr simulates the advanced female mode and increasing female abundance with increasing age but results in overall male dominance; (c) delayed female maturation and male mortality increased to 1.7 compared with the female rate of 0.9 does not account for overall female dominance; (d) delayed female maturation and a shift in the sex ratio of recruits to 20:80, males to females, simulates population structures at very low density (Fig. 1c).

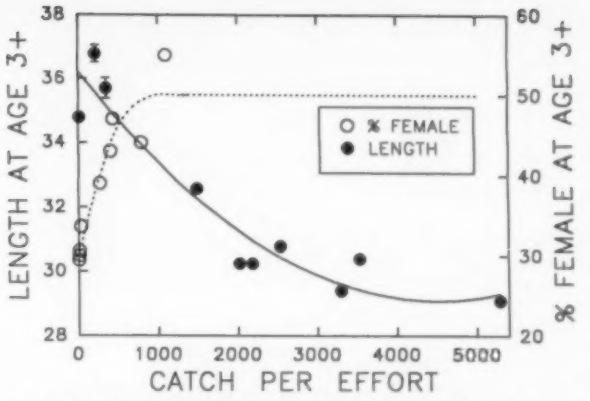

FIG. 4. Relationship between population density as measured by catch per effort (fish·km net^{-1}·night^{-1}) and total length at capture for age 3+ lake herring and percentage of females at age 3+ in Lake Superior. Confidence limits (95%) to mean lengths are given for the three populations at the lowest densities (those sampled in the present study). The solid line (length) is a second-order regression; the broken line (percentage of females) was fitted by eye.

age classes 1+ through 6+ and to age class samples comprising 10 or more individuals. We found that the extent to which adult lake herring populations depart from an overall 50:50 sex ratio is directly proportional to the slope of increasing female dominance with increasing age (Spearman's rank correlation, $P = 0.002$) (Fig. 5). Thus, this result establishes the existence of a strong link between delayed female maturation and overall female dominance. Although delayed maturation does not directly cause overall female dominance, it is linked to female dominance through a second, density-related population variable.

Recruitment Failure Effects on Population Structure

One population phenomenon that could contribute to overall female dominance is recruitment failure. If age classes being recruited to the spawning population are small relative to those in previous years, then the population would be composed largely of the older age classes which, at low densities, are dominated by females. This is likely to be a factor in extreme cases of female dominance (>90% female) in remnant lake herring populations that include no individuals in the younger age classes (Wright 1972).

In the more common cases of female dominance, females make up 55–75% of the adult population. This condition has been known to persist for a decade or longer (Dryer and Beil 1964; Peck 1975; Wright 1972). Results from the population structure model cast considerable doubt on the importance of recruitment failure in these populations. Not only does declining year class strength increase the proportion of the population made up of older fish, it reduces the apparent mean adult mortality rate. Because each year class is smaller than that which went before it, a mean mortality rate estimate based on the number of adults at each age at any one time would suggest an erroneously low rate. Within the model, continuous recruitment failure at 0.4 of the replacement value and effective adult mortality at 0.8 produces an apparent mean adult mortality rate of 0.1. In order to achieve an apparent mean adult mortality rate of 0.8, an effective rate of 1.7 is required. Although this produces a model population with 79% females, 1.7 is much higher

TABLE 2. Percentage of females in the population and percentage of females in each age class reported for populations of *C. artedii*. Slope values are from the linear regression of percentage of females at age as a function of age. The analysis was limited to age classes 1+ through 6+ and to age class samples containing 10 or more individuals.

Authority	Lake	Population % females	Age class % females						Slope
			1	2	3	4	5	6	
Cooper 1936	Blind	29		35	29	24	30	20	−2.9
Hile 1936	Trout	73		62	67	73	93	92	8.6
Hile 1936	Silver	55	52	62	56	53	56	67	1.5
Hile 1936	Clear	51	42	47	48	46	45	50	0.9
Fry 1937	Nipissing	53		51	53	52	60	59	2.3
Eddy and Carlander 1942[a]	Gull	63				52	65	71	9.5
Carlander 1945	Lake of the Woods	54	48	49	54	59	63	67	4.1
Smith 1956	Michigan, Green Bay	51		40	47	53	59		6.3
Dryer and Beil 1964	Superior, Duluth	58		41	60	74	83		14.0
Dryer and Beil 1964	Superior, Bayfield	57		47	60	62	69		6.8
Dryer and Beil 1964	Superior, Keweenaw	55		48	58	58	63		4.5
Dryer and Beil 1964	Superior, Marquette	37		45	35	36	39		−1.7
Present study	Superior, Keweenaw	75			26	54	72	92	21.6

[a]Cited in Smith (1956, table 33).

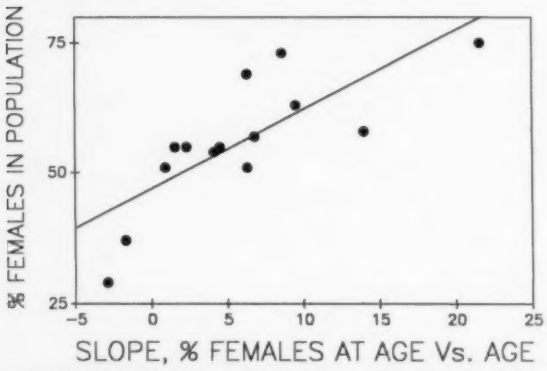

FIG. 5. Relationship between the rate at which females become increasingly dominant with age and overall femaleness in the population. Each point represents a different population except for one pair that represent the Keweenaw population separated by >20 yr (Table 2). Spearman's rank correlation analysis, a test insensitive to outliers, shows that the correlation between these two variables is significant at $P = 0.002$.

than mean rates found for unexploited populations (Table 1). A further limitation to the probable importance of recruitment failure in shaping lake herring populations concerns the degree of recruitment failure required to produce female dominance. Incidental catch of lake herring in the *Coregonus hoyi* fishery in Keweenaw waters indicates that the population declined by an average factor of 0.87 per year from 1975 to 1980 (R. Schorfhaar, Michigan Department of Natural Resources, Region I Headquarters, Marquette, MI, pers. comm.). In order to create a model population with 75% adult females similar to that found in Keweenaw waters in 1980, an annual decline factor of 0.45 would be required. Thus, recruitment failure may result in extreme cases of female dominance for periods of a few years in which younger age classes are essentially absent, but it does not readily account for the more typical cases of continuing female dominance that span a decade or more.

Density-Related Change in Sex Ratio of Recruits to Spawning Populations

If neither recruitment failure nor higher mortality of adult males accounts for female dominance, then the summed recruitment from a given age class to the adult population must be predominately female. There are two possible causes of female dominance within a year class prior to recruitment. Either juvenile males undergo higher mortality rates than juvenile females, or under conditions of low density the process of sexual differentiation results in predominately female lake herring. Although these cannot be distinguished in terms of the present data and model, one seems to be more likely to account for the general relationship between increasing percentage of females with age and overall female dominance.

Extrinsic sources of mortality such as predation, disease, and environmental stress are unlikely to occur with the constancy required to produce the observed pattern across many lakes and across years within lakes. Intrinsic sources of accelerated mortality that occur with such regularity are not likely to be favored by natural selection. Further, the population structure model indicates that a difference of 0.45 in male and female juvenile Z values is required to produce a spawning population of 75% females. Given the values found for Lake Superior populations (Table 2; Peck 1975), a mean difference as large as this seems unlikely.

Production of predominately female lake herring under specific conditions appears to be a more realistic possibility. Sex determination is more labile in teleosts than in other vertebrates and for some species is known to involve both genetic and environmental factors (Chan and Yeung 1983). Although the primary determinants of sex are genetic, the transformation from genotypic sex to phenotypic sex (the process of sexual differentiation) is a biochemical process that is susceptible to environmental influence. In some teleosts, sexual differentiation is not complete until well into the juvenile phase, and both physical (Conover and Kynard 1981) and behavioral or social (Chan and Yeung 1983) factors have been shown to influence the proportions of males and females produced. The timing of sexual differentiation in lake herring is not known. Fishery biologists with many years of experience examining age 0+ and 1+ lake herring are unable to distinguish sexes by macroscopic examination of the gonads (J. Selgeby, U.S. Fish and Wildlife Service, Ashland, WI, pers. comm.). To the extent of our knowledge, the necessary histological study has not been made. Data presented here for low-density conditions indicate that individuals that mature at age 3+ enter the adult population predom-

inately as males (Fig. 4) whereas those that defer maturation to ages 5+ and 6+ enter the adult population predominantly as females (Fig. 1c and 2). The population structure model indicates that with full female maturation delayed to age 6+, constant recruitment, and equal mortality rates for males and females, a ratio of four females to one male at sexual differentiation will result in a spawning population of 75% females. Thus, as density declines below an approximate CPE of 1000, an increasingly larger proportion of each year class enters the adult population as older females. The weight of available evidence suggests that sexual differentiation at low density produces many more females than males. This suggestion is consistent with results of experiments with other coregonid species. Larvae of *Coregonus lavaretus* (Worniallo and Mamcarz 1985) and *C. peled* (Mamcarz and Worniallo 1985) reared for 3 yr in cage culture at densities considerably above those expected in nature produced 12% females and 33% females, respectively. Nonetheless, given the current limitations of our knowledge, the possible role of higher mortality of juvenile males cannot be dismissed entirely.

Production Variables: Growth and Fecundity in Relation to Population Density

Comparison of mean total length at age 3+ for the 1978 year class collected at three sites indicates that growth rate was not clearly correlated with population density across the relatively narrow range of CPE's from 16 to 350. However, inclusion in the analysis of data for samples collected from 1950 to 1959 when populations were at much higher densities shows that over this expanded range, total length at age 3+ has a strong inverse correlation with density (Fig. 4).

Fecundity of lake herring females collected in Keweenaw waters in 1983 at a CPE of 7 averaged 50.2 eggs·g body weight^{-1} (N = 25, SD = 8.10, 95% confidence interval I: 3.34). Fecundity was not correlated with fish weight. In contrast, Dryer and Beil (1964, table 39) reported a mean fecundity of 29.7 eggs·g^{-1} for 30 lake herring collected at Keweenaw Bay and Marquette during 1950–54 at an average CPE of 2884. Although these authors gave no measure of dispersion in their data, this mean lies nearly 2.5 standard deviations below the low-density mean of 50.2, and thus this comparison indicates that fecundity is much higher at low population density.

Consequences of Density-Dependent Growth and Maturation for Individual Fitness

The relationship between growth and population density gives some indication of why fitness of females in low-density populations may be increased by deferred maturation. Fitness can be estimated as the product of the probability of survival to age x (l_x) and the egg production at age x (m_x), summed over all ages (Elseth and Baumgardner 1981, p. 274). As shown above, egg production for one spawning season may be taken as a constant proportion of female weight. Age of maturation has a direct effect on fitness. Earlier maturation has the benefit that probability of survival is greater. Later maturation has the benefit that the female will have grown to a larger size and thus egg production will be greater. The age of maturation at which fitness ($l_x m_x$ summed for all ages) is maximized depends on the specific mortality and growth functions that apply to a given condition.

We calculated $l_x m_x$ for maturation at ages 2+ through 9+ using size at age data reported by Dryer and Beil (1964) for

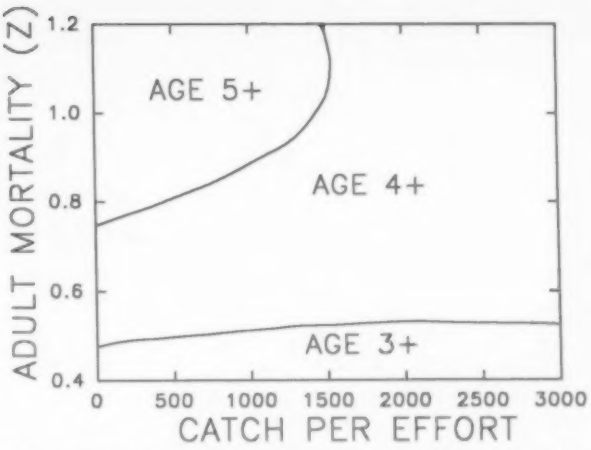

FIG. 6. Age of maturation at which fitness is maximized for various combinations of adult mortality rate (Z_a) and population density (catch per effort). See text for details.

waters off Bayfield, WI (CPE = 3000), and Marquette (CPE = 1500) during 1955–61 and using our own data for Keweenaw waters in 1980 at CPE = 7. Individual calculations were made for adult mortality rates of 0.4, 0.6, 0.8, 1.0, and 1.2 at each density. Whereas rates of 0.8–1.0 appear to apply to unexploited Lake Superior stocks in the early 1980's (Table 1), rates >2 were typical under conditions of exploitation during the 1960's (Peck 1975). Juvenile mortality rate was taken as 0.2. For each density and mortality rate combination, we determined the age at which $l_x m_x$ was greatest (t_{max}). A second-order polynomial was fitted to t_{max} values as a function of CPE and adult mortality rate (Fig. 6, regression ANOVA P = 0.001). The analysis shows that growth and mortality functions which best describe Lake Superior lake herring are of the form and dimension necessary for there to be a fitness benefit from deferred female maturation. In particular, our calculations indicate that deferred female maturation will increase fitness at very low population densities, but not at higher densities (Fig. 6). This conclusion is dependent on the assumption that Z_j is approximately 0.2 and thus deferred maturation does not greatly decrease survival to maturation. A value of Z_j = 0.5 does not indicate a benefit to fitness from deferred maturation.

Consequences of Density-Dependent Fecundity, Growth, Maturation, and Adult Sex Ratio for Population Recovery

Changes in fecundity, growth, maturation, and adult sex ratio that characterize lake herring at low densities all contribute to increased egg production per individual in the population. The precollapse population in Keweenaw waters during 1950–54 produced 2840 eggs per individual, compared with 13 860 eggs per individual produced by the 1980 population. Contributions to this 4.88-fold increase were as follows: fecundity, 1.69; growth, 1.63; deferred maturation, 1.18; and female dominance, 1.50. It has long been known that lake herring year class strength is highly variable, often with many years elapsing between strong year classes. The apparent density-dependent responses seen here may have evolved to compensate for such variable recruitment.

The contribution of this apparently compensatory response to recovery of collapsed lake herring populations is modulated by other factors that influence year class strength. Two excep-

tionally strong year classes have been produced since 1970, one in 1978 and one in 1984 (J. Selgeby, pers. comm.). The 1978 year class entered the three populations we sampled in 1981 as age 3+ fish (Fig. 2). In Keweenaw waters, they entered at a low CPE of 23, males were twice as abundant as females, and the overall Keweenaw population structure remained typical of a collapsed population for the years 1981–83. In Duluth waters, the 1978 year class entered the population at a much higher CPE of 949, and by 1983 an apparently healthy age structure comprising ages 3+ through 5+ with roughly 50% females at each age and exactly 50% females in all three ages combined was established at a CPE of 754. Nonetheless, neither of these populations appears to have grown significantly until the entry of the 1984 age class (R. Schorfhaar, Michigan Department of Natural Resources, pers. comm.; D. Schreiner, Minnesota Department of Natural Resources, Duluth, MN, pers. comm.).

A striking feature of lake herring recruitment in Lake Superior is the similarity of year class strength for a given year class across a distance of hundreds of kilometres spanning many discrete populations. The 1978 year class recruited at age 3+ was a similar proportion of the total population in Duluth, Marquette, and Keweenaw waters (Fig. 2). Dryer and Beil (1964) also found an impressive correlation between the strength of year classes in Duluth, Keweenaw, and Bayfield waters from 1946 to 1955. Future efforts to better understand the population dynamics of *C. artedii* may benefit most from investigation of factors that determine the survival of larvae and juveniles.

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Mitochondrial DNA Variation Reveals Genetically Distinct Sympatric Populations of Anadromous and Nonanadromous Atlantic Salmon, *Salmo salar*[1]

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Birt, T. P., J. M. Green, and W. S. Davidson. 1991. Mitochondrial DNA variation reveals genetically distinct sympatric populations of anadromous and nonanadromous Atlantic salmon, *Salmo salar*. Can. J. Fish. Aquat. Sci. 48: 577–582.

Mitochondrial DNA variation was surveyed among wild anadromous and nonanadromous Atlantic salmon, *Salmo salar*, which occur in sympatry in Gambo River, Newfoundland. Seventy-one salmon were screened with 18 restriction enzymes, 5 of which revealed nucleotide sequence variation. Nucleotide sequence divergence estimates among the four distinct genotypes detected ranged from 0.2 to 1.0%. Significant heterogeneity in mtDNA genotype frequencies supports the view that exchange of breeding females between groups is infrequent or does not occur, an inference consistent with the observation that the forms use separate spawning sites within the system. Mitochondrial DNA diversity was somewhat greater among the nonanadromous salmon than the anadromous salmon (nucleon diversity (h) = 0.37 and 0.52, respectively). Potential mechanisms for maintaining reproductive isolation include selection of different spawning habitats, different spawning times, and sexual selection based upon the size difference between the two forms.

On a étudié la variation de l'ADN mitochondrial chez des saumons de l'Atlantique sauvages, *Salmo salar*, anadromes et non anadromes, qui vivent en sympatrie dans la rivière Gambo (Terre-Neuve). Chez 71 saumons mis en présence de 18 endonucléases de restriction, 5 individus ont montré des variations de la séquence des nucléotides. Les estimations de la divergence de la séquence des nucléotides chez les quatre génotypes distincts relevés varient de 0,2 à 1,0 %. L'hétérogénéité significative des fréquences du génotype de l'ADN mitochondrial soutient l'hypothèse que l'échange de femelles génitrices entre les groupes n'a pas lieu ou est peu fréquent; cette déduction est compatible avec l'observation que les deux formes utilisent différentes frayères au sein du système fluvial. La diversité de l'ADN mitochondrial était légèrement plus élevée chez les saumons non anadromes par rapport aux saumons anadromes (diversité des nucléons (h) = 0,37 et 0,52, respectivement). Les mécanismes potentiels pour le maintien de l'isolement reproductif comprend le choix de différentes frayères, de différentes périodes de fraie et le choix d'un partenaire sexuel basé sur la différence de taille.

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In Newfoundland, Atlantic salmon, *Salmo salar*, populations show great variation in migratory behaviour. Typical anadromous forms are found in most accessible rivers. In addition, physically landlocked populations occur in many lakes and ponds throughout the province. These salmon often mature at very small body size and hence are sometimes referred to as dwarf forms (Leggett and Power 1969; Bruce 1976; Barbour et al. 1979; Sutterlin and MacLean 1984). A third, intermediate situation is also common in which anadromous and nonanadromous salmon occupy the same river. Access to the sea is not prevented by physical barriers to migration and the two forms are not prevented from mingling freely throughout all or much of the system (Couturier et al. 1986; Hutchings 1986; Verspoor and Cole 1989). The latter situation presents a problem for fishery biologists because, for effective management, it is necessary to know whether such forms represent separate gene pools or alternatively whether gene flow occurs.

The objective of this study was to determine if genetic differences are present between sympatric anadromous and nonanadromous Atlantic salmon and whether the two forms are reproductively isolated. Electrophoretically detectable protein variation in this species is low. Gene frequencies have been estimated at more than 60 loci in some Atlantic salmon populations. However, more than 95% of the variation is accounted for by only four loci. Previous studies using this technique for stock discrimination have generally met with limited success (for reviews see Ryman 1983; Ståhl 1987; Davidson et al. 1989a). For this reason, mitochondrial DNA (mtDNA) was chosen as a potentially more informative genetic system for analysis.

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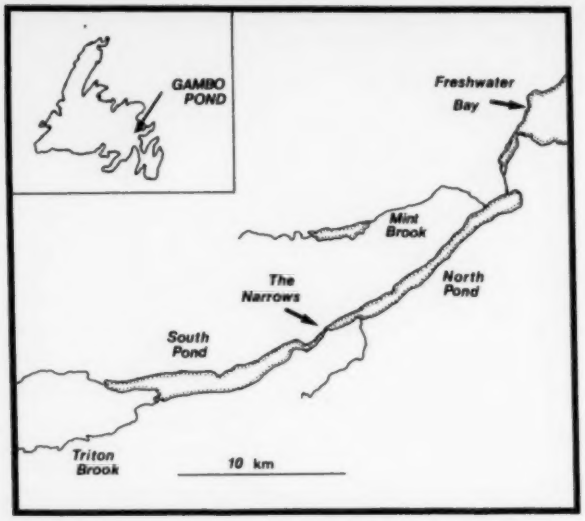

FIG. 1. Map of Gambo Pond showing locations of major tributaries.

Methods and Materials

Study Area

Gambo Pond (48°37′N, 54°24′W), an oligotrophic lake in eastern Newfoundland, actually consists of two long narrow lakes separated by a short stretch of river (the narrows). As described by Leggett and Power (1969), Gambo Pond North has a surface area of approximately 1100 ha and a maximum depth of 12 m; Gambo Pond South is slightly smaller in area (950 ha) but deeper (maximum depth of 40 m). Gambo Pond North is drained by Gambo River which runs for approximately 2 km to Freshwater Bay. Two major tributaries empty into the system: Triton Brook enters Gambo Pond South near the southwest end and Mint Brook enters near the outlet of Gambo Pond North (Fig. 1).

In October 1986, mature anadromous salmon were seined from pools in Triton Brook approximately 2 km upstream of the outlet into Gambo Pond South. Adult nonanadromous salmon were angled and fyke netted at this time in Gambo Pond North near the outlet. Adults of the two forms were very easily differentiated: nonanadromous salmon were smaller (29.8–39.6 cm fork length, $N = 18$) than anadromous fish (45.8–64.0 cm fork length, $N = 21$). The former were much darker in colour and had larger heads. In no instance was the identity of any fish in doubt. Salmon were transported alive to the Ocean Sciences Centre where they were held in tanks until required for mtDNA preparation.

Mitochondrial DNA

Preparation of mtDNA was carried out using two methods: the alkaline extraction method (Palva and Palva 1985) and by density gradient centrifugation (Carr and Griffith 1987). Purified mtDNA samples were digested with 18 restriction endonucleases (*Bam*HI, *Bgl*I, *Bgl*II, *Bst*EII, *Dra*I, *Eco*RI, *Eco*RV, *Hinc*II, *Hind*III, *Hpa*I, *Pst*I, *Pvu*II, *Sac*I, *Sac*II, *Sal*I, *Sma*I, *Xba*I, and *Xho*I) according to the manufacturer's directions. Restriction fragments were end-labelled according to the following adaptation of the protocol of Brown (1980). Ten nanograms (or less) of mtDNA was digested to completion in a volume of 15 μL. To the reaction mixture was added 2 μL of a cocktail containing 65 μM dGTP, dATP, and dTTP, 400 mM Tris–HCl (pH 7.5), 80 mM $MgCl_2$, 0.65 mM dithiothreitol, 0.5 unit of DNA polymerase (Klenow fragment), and 1 μCi (37 kBq) of [α-^{32}P]dCTP. After incubation at room temperature for 10 min, DNA fragments were precipitated by the addition of 3 μL of tRNA (19 mg·mL^{-1}), 40 μL of sodium acetate (3 M, pH 5.8), 350 μL of water, and 900 μL of cold 95% ethanol. Tubes were chilled at −70°C for 20 min, centrifuged (10 000 × *g*) for 5 min, and decanted and the pellets were washed three times with cold 70% ethanol, desiccated, suspended in 20 μL of buffer containing 50% glycerol and bromophenol blue, and loaded into vertical 1–1.5% agarose gels. Following electrophoresis, gels were dried and autoradiographed overnight.

Southern blotting was used for a few samples which were seriously contaminated with nuclear DNA. Following electrophoresis in horizontal agarose gels, mtDNA fragments were denatured in 1.5 M NaCl/0.5 M NaOH and transferred to nylon membranes (Hybond N, Amersham). Blots were then prehybridyzed and probed with ^{32}P-labelled mtDNA (prepared from ripe oocytes of capelin, *Mallotus villosus*) according to the procedure described by Cutler et al. (1991). In general the heterologous capelin mtDNA probe was satisfactory, but the signal produced by small fragments (<1 kilobase pair) was sometimes weak, presumably due to inefficient binding of such fragments to the nylon membranes. For restriction enzymes with hexanucleotide recognition sequences, capelin mtDNA was a suitable probe.

For statistical comparison of mtDNA genotype frequencies between anadromous and nonanadromous salmon, the randomized chi-square test described by Roff and Bentzen (1989) was used.

Results

The restriction endonucleases used in this survey and the fragment patterns generated are shown in Table 1. All enzymes cleaved Atlantic salmon mtDNA at least once. A total of 57 restriction sites were detected. By summing the sizes of fragments generated by various enzymes, it is estimated that the mitochondrial genome of this species contains approximately 16.7 kilobase pairs. This estimate is in agreement with previous studies (Birt et al. 1986; Gyllensten and Wilson 1987; Palva et al. 1989). A restriction site map for Atlantic salmon mtDNA has been published previously (Davidson et al. 1989b).

Five restriction endonucleases revealed nucleotide sequence variation (Table 1). Figure 2 illustrates variant restriction fragment profiles produced by the enzymes *Bgl*II and *Pvu*II. Variant patterns could be accounted for by the loss or gain of single sites. It is assumed that site gains and losses are due to single-base substitutions. Evidence for heteroplasmy or length polymorphism was not observed. Restriction fragment patterns generated by individual enzymes were assigned uppercase letter designations. Each salmon was then assigned a composite mtDNA genotype by combining information from each enzyme. Four such genotypes were observed among the 71 Atlantic salmon screened for all 18 restriction enzymes (Table 2). Lineage diversity, as indicated by the nucleon diversity index (*h*, Nei and Tajima 1981), appeared to be greater among the nonanadromous salmon (Table 2).

Estimates of the nucleotide sequence divergence between genotypes were calculated separately from restriction fragment

TABLE 1. Fragment patterns generated by restriction endonucleases used to screen anadromous and nonanadromous Gambo Atlantic salmon mtDNA.

1 *Bgl*II		2 *Bst*EII		3 *Dra*I		4 *Hinc*II	
A	B	A	B	A	B	A	B
16.7	15.8	16.7	10.2	10.2	8.5	4.1	4.1
	0.86		6.5	6.0	6.0	3.45	3.45
				0.65	1.7	2.4	2.4
					0.65	1.8	1.8
						1.7	1.15
						0.95	0.95
						0.75	0.75
						0.65	0.65
						0.60	0.60
						0.56	0.56
							0.55

5 *Pvu*II		6 *Bam*HI	7 *Bgl*I	8 *Eco*RI	9 *Eco*RV	10 *Hind*III
A	B	A	A	A	A	A
6.8	9.3	10.1	5.5	7.9	13.1	9.0
3.5	3.5	6.6	5.5	4.9	1.7	4.2
2.6	2.6		4.3	4.0	1.6	3.5
2.5	1.4		1.2			
1.4						

11 *Hpa*I	12 *Pst*I	13 *Sac*I	14 *Sac*II	15 *Sal*I	16 *Sma*I
A	A	A	A	A	A
7.0	12.4	16.7	15.0	16.7	16.7
4.5	4.0		1.7		
3.6	0.3				
1.7					

17 *Xba*I	18 *Xho*I
A	A
5.1	16.7
3.7	
3.4	
2.4	
2.1	

patterns generated by enzymes with six-base recognition sequences and by *Hinc*II using equation 16 from Nei and Li (1979; the "site method"). Overall estimates of percent sequence divergence among genotypes were calculated from the two separate estimates by weighting according to the number of nucleotides surveyed (Table 3). Pairwise sequence divergence estimates among the four genotypes range from 0.2 to 1.0%.

Presence or absence of the variable sites (generated by the enzymes *Bgl*II, *Bst*EII, *Dra*I, *Hinc*II, and *Pvu*II) in the four genotypes observed is shown in Table 4. Figure 3 shows an unrooted network, produced using the parsimony method, which links the genotypes. The genotypes fall into two clusters due to the perfect association of alternative fragment patterns produced by the enzymes *Bgl*II, *Bst*EII, and *Dra*I. All genotypes displayed either the "A" pattern or the "B" pattern for these three enzymes.

Two mtDNA genotypes were observed among the anadromous Atlantic salmon, while four genotypes occurred among the nonanadromous salmon (Table 2). Genotype 1 was the most prevalent mtDNA type and occurred in 76 and 67% of anadromous and nonanadromous salmon, respectively. Genotype 2 was more common among anadromous salmon, while genotypes 3 and 4 were observed only among nonanadromous salmon. Genotype frequencies differed significantly between the behaviourly different forms ($p < 0.001$; Table 4). These results indicate that little or no female-mediated gene flow occurs between these populations.

Discussion

Mitochondrial DNA is a more sensitive indicator of population structuring than protein electrophoresis. This has been illustrated in studies of other organisms in which mtDNA analysis was conducted in conjunction with protein electrophoresis (Avise et al. 1984; Ward et al. 1989).

Little information concerning mtDNA variation in Atlantic salmon has been published. A limited survey of two allopatric populations in Newfoundland (one anadromous, one nonanadromous) revealed almost no variation (Birt et al. 1986). In another survey, Palva et al. (1989) found differences in mtDNA of anadromous salmon from the Neva River and nonanadromous salmon from the River Pielisjoki, Finland. Hovey et al. (1989) screened 40 salmon from the River Itchen in southern England for approximately 150 restriction sites generated by eight enzymes. Three of these enzymes produced variable fragment patterns and a total of six mtDNA genotypes were observed. Gyllensten and Wilson (1987) detected a low level of nucleotide sequence difference (0.12%) between two hatchery populations of Swedish salmon.

Evidence for large-scale population structuring of mtDNA variation in Atlantic salmon was reported by Bermingham et al. (1988). These authors characterized western and eastern Atlantic populations based on 47 salmon sampled from hatcheries operated in the northwestern United States. North American and European mtDNA genotypes were found to differ by at least seven restriction sites, and fixed differences were revealed by five enzymes. This information was then used to correctly identify the continent of origin for 67 of 68 salmon which had been tagged as smolts (thus, their rivers of origin were known) and subsequently caught in the west Greenland fishery. Results of the present study are inconsistent with this pattern, since both "European" and "North American" genotypes were observed among the Gambo salmon. Restriction fragment patterns generated by three enzymes (*Bgl*II, *Bst*EII, and *Dra*I) do not distinguish eastern and western Atlantic mtDNA genotypes, as suggested by the data of Bermingham et al. (1988). Furthermore, "European" genotypes have been found in additional salmon populations in Newfoundland and in populations in Nova Scotia and Quebec (H. P. McVeigh, S. E. Bartlett, and W. S. Davidson, unpubl. data). Further sampling of populations from rivers throughout the range of the species is clearly required to attain a better understanding of mtDNA variation in Atlantic salmon. Until this is achieved the utility of mtDNA for stock discrimination will remain unknown.

Results of this study support the hypothesis that anadromous and nonanadromous salmon in the Gambo system belong to separate reproductive units and should therefore be managed as separate stocks. The various mtDNA genotypes are present in the two groups in significantly different frequencies, demon-

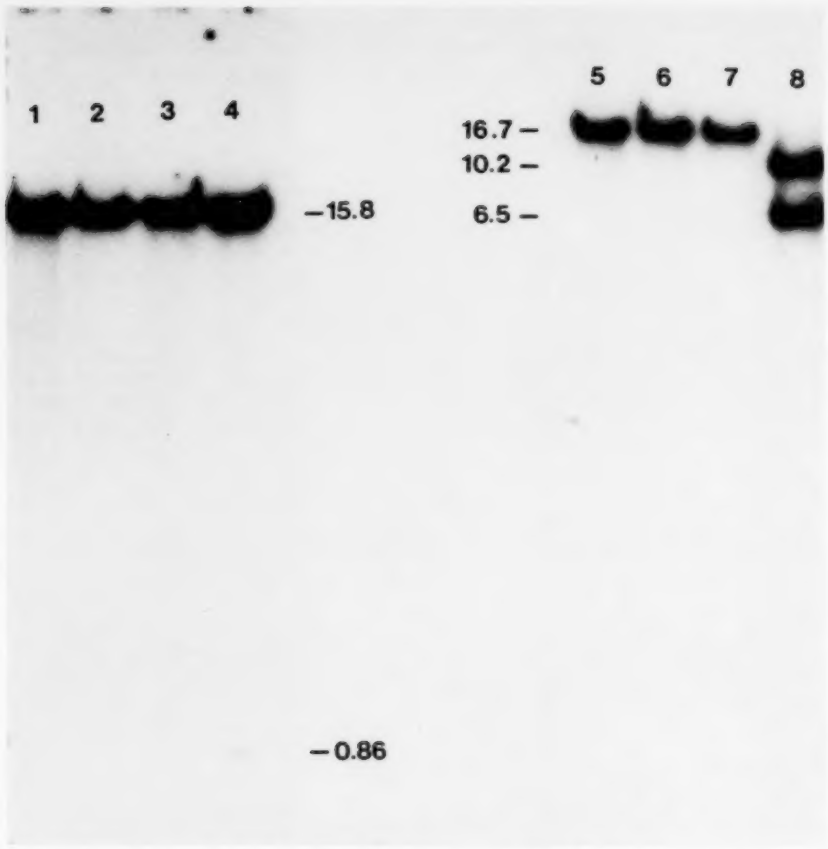

FIG. 2. Autoradiogram of end-labelled restriction fragments produced by the enzymes *Bgl*II ("A" pattern, lanes 1–3; "B" pattern, lane 4) and *Bst*EII ("A" pattern, lanes 5–7; "B" pattern, lane 8). Fragment sizes are indicated in kilobase pairs.

TABLE 2. Distribution of mtDNA genotypes among Gambo anadromous and nonanadromous Atlantic salmon. Letters in each composite genotype represent the fragment patterns generated by individual restriction endonucleases that produce variable patterns. Enzymes are numbered as shown in Table 1. The nucleon diversity index (h) is also given for the two forms.

	Endonuclease							
Genotype	1	2	3	4	5	Anadromous	Nonanadromous	
1	A	A	A	A	A	28	23	
2	B	B	B	A	A	9	1	$\chi^2 = 16.7$
3	A	A	A	B	A	0	6	$p < 0.001$
4	B	B	B	A	B	0	4	
h						0.37	0.52	

TABLE 3. Percent sequence divergence estimates for mtDNA genotypes observed among Gambo Atlantic salmon (above diagonal). The number of restriction sites observed in each genotype is shown on the diagonal. Entries below the diagonal indicate the number of sites shared by genotype pairs.

	Genotype			
Genotype	1	2	3	4
1	53	0.4	0.2	0.8
2	53	56	0.6	0.2
3	53	53	54	1.0
4	52	55	52	56

strating that successful exchange of breeding females is infrequent (assuming no selective advantage among genotypes). That the two forms are reproductively isolated is further supported by genetically determined developmental and physiological differences observed among cultured salmon of the two forms from this same watershed (Birt 1990).

There is evidence that reproductive isolation is maintained by both temporal and spatial mechanisms in this system. Adult females used as broodfish in a culture experiment (Birt 1990) did not ovulate at the same time. Despite being caught in the Gambo system at the same time (late October), anadromous females ovulated at least 3 wk earlier than nonanadromous females. The times at which the two forms spawn naturally in the Gambo system are not known, but it is conceivable that a 3-wk difference in spawning times could restrict gene flow between the populations. Temporal reproductive isolation among sympatric salmonine populations has been reported in Arctic char, *Salvelinus alpinus* (Child 1984), and rainbow trout, *Oncorhynchus mykiss* (Leider et al. 1984).

Anadromous and nonanadromous salmon in Gambo Pond use different areas of the system as spawning sites. The most

TABLE 4. Presence (+) or absence (−) of variable restriction sites in each of the four salmon mitochondrial genotypes. Genotypes are numbered as in Table 2.

	Genotype			
Enzyme	1	2	3	4
*Bgl*II	−	+	−	+
*Bst*EII	−	+	−	+
*Dra*I	−	+	−	+
*Hinc*II	−	−	+	−
*Pvu*II	+	+	+	−

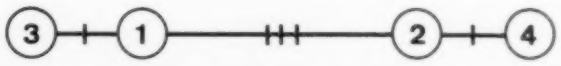

FIG. 3. Unrooted network connecting salmon mitochondrial genotypes constructed using the parsimony method. Verticle crossbars represent restriction site differences between genotypes. Genotypes are numbered as in Table 2.

important spawning river in the system for anadromous fish is Triton Brook, the major tributary of Gambo Pond South, whereas nonanadromous salmon spawn at the outlet of Gambo Pond North. Salmon also spawn elsewhere within the system. Approximately 25–40% of the anadromous salmon in the system spawn in Mint Brook. In addition, redds have been observed in gravel beds at the narrows and spawning is also suspected in Parson's Brook (Porter et al. 1974). From what is known about the distribution of reproductive activity throughout the system, it appears that spawning habitat utilized by anadromous salmon is typical of that normally associated with the species, i.e. areas of river flowing over gravel (Jones 1959). In contrast, the nonanadromous salmon appear to deposit their eggs in areas of reduced flow, specifically near the outlet of Gambo Pond North where the bottom substrate consists mainly of large rocks and boulders. Thus, different habitat selection at spawning time might effectively limit gene flow between the populations to the degree that heterogeneity of mtDNA genotype frequencies is maintained. Couturier et al. (1986) have reported evidence suggesting that sympatric anadromous and nonanadromous salmon select different areas within North Arm River, Newfoundland, as spawning sites. Furthermore, these authors determined that nonanadromous salmon (which spawn at a pond outlet in this system) scatter their eggs among boulders, in contrast with anadromous salmon which deposit their eggs in redds excavated in gravel substrate. Cowan and Baggs (1988) described lacustrine spawning by nonanadromous salmon in another Newfoundland watershed. Thus, the two forms may select different spawning habitat in many rivers, and at least some nonanadromous salmon are egg scatterers rather than redd builders. However, these different reproductive behaviours are not universal among nonanadromous salmon, since redd building in riverine habitat has been reported elsewhere (Havey and Warner 1970).

Assortative mating based upon size could also act as an isolating mechanism. This phenomenon has been reported in sympatric populations of anadromous and nonanadromous sockeye salmon, *Oncorhynchus nerka* (Foote and Larkin 1988), but there is no evidence of such sexual selection in Atlantic salmon.

While nonanadromous spawners appear to be confined to the area near the outlet of Gambo Pond North, anadromous salmon in the system are not restricted to spawning sites in Triton Brook. Several mature anadromous adults were captured at the lake outlet while angling for nonanadromous fish. It was possible that these salmon were simply passing through the area when captured and would have spawned elsewhere in the system. Alternatively, anadromous and nonanadromous salmon may spawn at this same locality in the pond and interbreed freely. If this is the case, then the apparent separation of gene pools suggested by the mtDNA analysis is not based primarily upon an anadromous/nonanadromous dichotomy, but rather on reproductive isolation resulting from strong fidelity to different spawning sites. This hypothesis implies that at least two salmon stocks occupy the Gambo system and that alternative life histories (anadromy versus residency) are employed by individuals of the largely nonanadromous stock (see Gross 1984).

Another possibility is that assortative mating could occur at the pond outlet as it does among sympatric sockeye and kokanee (Foote and Larkin 1988). This would imply that the anadromous/nonanadromous dichotomy is the basis for the separation of gene pools. Under this hypothesis, anadromous salmon spawning at the pond outlet may or may not belong to the Triton Brook spawning population. It is conceivable that several distinct salmon stocks are present in the Gambo system. However, it is not known if homing behaviour among spawners is sufficiently accurate to maintain reproductive isolation.

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Composition and Mechanics of Routine Swimming of Rainbow Trout, *Oncorhynchus mykiss*

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Routine swimming encompasses all volitional motions of fish. It is usually assumed to be quasi-steady, i.e. routine swimming is mechanically equivalent to steady swimming. Routine swimming of rainbow trout, *Oncorhynchus mykiss*, was dominated by unsteady motions of linear and centripetal (angular) acceleration. Constant-speed swimming was rare. Mean speeds and acceleration rates were small. Tail-beat frequencies were nevertheless strongly correlated with mean swimming speed, but increased more rapidly with increasing speed in routine swimming than in steady swimming. Tail-beat amplitudes and propulsive wavelengths were similar to values seen in steady swimming. The composition of routine swimming and analysis of the force balance showed that routine swimming was not quasi-steady. Therefore, forces and rates of working should be estimated from a complete description of whole-body deformation. This is impractical. Drag dominated resistance in routine swimming, such that average thrust (= resistance) may be computed from mean speed and/or averaged kinematic variables for the trailing edge with a correction factor of approximately 3. Analysis of routine swimming may permit comparisons among a wider range of vertebrates than possible with commonly used methods.

Les mouvements de nage habituels des poissons sont tous volontaires. On les suppose généralement comme étant quasi permanents, c'est-à-dire qu'ils sont mécaniquement équivalents à une nage constante. Les mouvements de nage habituels de la truite arc-en-ciel, *Oncorhynchus mykiss*, sont caractérisés par des mouvements irréguliers d'accélération linéaire et centripède (angulaire). Les déplacements à vitesse constante sont rares, tandis que les vitesses moyennes et les taux d'accélération sont faibles. Toutefois, les fréquences de battement de la queue sont étroitement liées à la vitesse moyenne de nage; par contre, elles augmentent plus rapidement en fonction d'une vitesse croissante pendant les mouvements habituels de nage que pendant les mouvements constants de nage. L'amplitude des battements de la queue et la longueur d'onde de propulsion sont semblables aux valeurs observées pendant la nage constante. La composition de la nage habituelle et l'analyse de l'équilibre des forces ont révélé que la nage habituelle n'est pas quasi permanente. Les forces et les taux de travail devraient donc être déterminés à partir d'une description complète de la déformation corporelle globale. Mais ceci est impratiquable. La résistance contrôlée par l'effet d'entraînement au cours des mouvements de nage habituelle signifie que la poussée moyenne (= résistance) peut être calculée à partir de la vitesse moyenne et/ou des variables cinématiques moyennes de la partie arrière, avec un facteur de correction d'environ 3. L'analyse des mouvements de nage habituelle pourrait permettre de les comparer chez un plus grand nombre de vertébrés que ne le permettent les méthodes courantes.

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Studies on the mechanics of vertebrate locomotion have focussed on fish either swimming at relatively constant rectilinear speeds (steady swimming) in cruising and sprinting or during high rates of linear and centripetal acceleration (unsteady swimming) in fast-starts and powered turns. These do not appear to be the dominant components of *routine swimming* (Nursall 1958; Major 1978; Eaton and Hackett 1984; Vinyard 1982; Webb 1984, 1986; Fuiman and Webb 1988), where routine swimming is defined as volitional movements in such activities as feeding, territorial defence, and other agonistic behaviors, courtship, etc. Nevertheless, routine swimming is treated as if it were steady swimming. Expressed formally, this quasi-steady assumption presumes that thrust and resistance during routine swimming at any given average speed are equal to the average thrust and drag during rectilinear swimming at the same constant speed. Furthermore, time-varying motions of accelerations in routine swimming are implicitly assumed to have a negligible effect on forces, kinematics, and performance. As an example of the quasi-steady assumption, swimming performance in the field is typically measured only as distance travelled or mean speed (e.g. Young et al. 1972; Holliday et al. 1974; Sciarrotta and Nelson 1977; Diana 1980). Consequently, results from studies of the mechanics and energetics of steady swimming have been used to estimate costs of routine swimming (e.g. Feldmeth and Jenkins 1973; Ware 1975, 1978; Kerr 1982; Feldmeth 1983).

Recent studies suggest that unsteady motions are associated with substantial increases in energy costs compared with steady swimming at the same average speed (Weatherley et al. 1982; Puckett and Dill 1984, 1985; Weatherley and Gill 1987). This implies that routine swimming is not quasi-steady. If so, the usual methods of studying and reporting locomotion of free-

swimming fish may be inappropriate. Therefore, the purpose of this work was to evaluate the hypothesis that routine swimming is quasi-steady.

Theory

Routine swimming is a general term for complex spatial displacements of an animal. These displacements are resolved at the center of mass of the body, the point about which propulsive forces act. The path of any point, such as the center of mass, in a plane is described in terms of state and control variables, velocity and acceleration, respectively. Thus the state of an object is described by its velocity, this being zero for a stationary object. Changes in state occur due to control variables of linear and centripetal (angular) acceleration (Isaacs 1975). Therefore, the minimal kinematic variables required to define body movements in routine swimming are velocity (or for practical purposes average speed), linear acceleration, and centripetal acceleration.

Work must be performed to overcome resistance to sustain motion and to accelerate. The resistance to constant-speed motion is the hydrodynamic drag, R_{drag} (Hoerner 1965):

$$(1)\quad R_{drag} = 0.5 \cdot \rho \cdot S \cdot u^2 \cdot k \cdot Cd$$

where Cd = reference drag coefficient, k = correction factor to Cd for swimming fish, ρ = density of water, S = wetted surface area, and u = swimming speed.

The reference drag coefficient is usually that for a dynamically similar flat rigid plate moving parallel to the flow. It is known that the swimming drag of a fish is 3–5 times larger than this reference, necessitating the correction factor k (Alexander 1967; Lighthill 1975; Webb 1975). The correction is assumed to be 4 here.

The drag coefficient depends on the nature of the flow in the boundary layer. The boundary layer is a thin region of flow over the whole surface where the water velocity decreases from the speed of the fish to the zero speed of the surrounding water. The viscous shear force is proportional to the velocity gradient. Therefore, the boundary layer is a region of velocity gradient and hence large viscous-related forces. Boundary layer flow is likely to be turbulent, as most fish swim routinely in water disturbed by other fish or in other turbulence. Then:

$$(2a)\quad Cd = 0.072 \cdot Re^{-0.2}$$

where Re is Reynolds number defined by

$$(2b)\quad Re = L \cdot u / \nu$$

where L = total length and ν = kinematic viscosity of water.

Inertial resistance to linear acceleration, R_{linear}, is given by

$$(3)\quad R_{linear} = (1 + \alpha) \cdot \rho_b \cdot V \cdot a$$

where α = added mass coefficient for the acceleration reaction contribution of water affected by the body and resisting linear acceleration (this contribution can be modelled by adding its mass to that of the body, and hence the term *added mass*), ρ_b = density of the body, a = linear acceleration rate, and V = body volume.

Inertial resistance to centripetal acceleration, $R_{centripetal}$, is given by (Daniel and Webb 1987)

$$(4)\quad R_{centripetal} = (1 + \beta) \cdot \rho_b \cdot V \cdot u^2 / r$$

where β = added mass coefficient for centripetal accelerations and r = turning radius.

The added mass coefficient is not known for linear or centripetal acceleration. Webb (1983) measured an added mass coefficient of 0.2 for fish during fast-starts, which are acceleration turns including both linear and centripetal accelerations. This value of 0.2 is assumed for both α and β.

Assuming that resistance components do not interact, and recognizing that $R_{centripetal}$ acts at right angles to drag and linear acceleration resistance, the net resistance, R, is (Weihs 1981)

$$(5)\quad R = \sqrt{[(R_{drag} + R_{linear})^2 + R^2_{centripetal}]}.$$

At every instant, net resistance is balanced by a thrust force (Daniel and Webb 1987). Thrust is generated by the body and fins. Most fish use lateral undulations of the body and caudal fin, except at very low speeds. Swimming with the body and caudal fin is considered here.

There are many theories that may be used to describe the mechanics of swimming depending on the shape, size, and swimming kinematics of a fish (Daniel and Webb 1987). Slender body theory developed by Lighthill and collaborators (Weihs 1972, 1973; Lighthill 1975) and by Wu and collaborators (Wu 1977; Yates 1983) is used to describe thrust for trout-like fishes swimming by body and caudal fin undulation. These subcarangiform fish typically move at high Reynolds numbers ($>10^3$), when inertial forces dominate. Acceleration reaction is the dominant propulsive force at high Reynolds numbers when a propulsor moves at high frequencies compared with the average forward velocity (Lighthill 1975; Wu 1977; Yates 1983; Daniel and Webb 1987). The importance of high-frequency movements relative to the mean forward motion is estimated using reduced frequency, calculated as $\omega \cdot L/u$, where ω is the radian frequency, $2 \cdot \pi / t$. Acceleration reaction becomes important with reduced frequency greater than 0.1 and dominates the force balance when greater than 0.4 (Daniel and Webb 1987). Reduced frequencies were always greater than 9 and averaged 24 for trout during routine swimming.

Slender body theory also recognizes that the body is laterally flattened to provide for the acceleration of large masses of water (Weihs 1989). Variation in the added water mass along the body length is reasonably small; added mass for lateral movements depends on the square of body and fin depth over those portions of the body making large lateral movements while gaps between fins are filled by a vortex sheet (Lighthill 1971). For steady swimming, lateral movements are just small enough that actual forces can be transferred to a centerline reference without too much error (Yates 1983).

Consider a fish moving along the x-axis while beating its tail along the z-axis. Each element along the body, a, with $a = 0$ at the trailing edge tip of the tail, accelerates water in its vicinity. Instantaneous thrust, T_i, is given by (Lighthill 1971):

$$(6)\quad T_i = \left(m \cdot w \cdot \frac{dz}{dt} - 0.5 \cdot w^2 \cdot \frac{dz}{da} \right)_{a=0} + \frac{d}{dt} \int_0^L m \cdot w \cdot \frac{dz}{da} \cdot da$$

where m = added mass of water per unit length, given by $\rho \cdot \pi \cdot B^2/4$ (B = body and fin span (depth)), dz/dt = lateral velocity of an element, with a mean value of $\pi \cdot H/t\sqrt{2}$ (H = lateral amplitude of an element and t = tail-beat period), and w = the velocity given to m, calculated as $(1 - u/c)dz/dt$ (c =

TABLE 1. Summary of morphological parameters for the trout studied (mean ± 2 SE, $n = 10$).

Total length, L (cm)	Mass (g)	Wetted surface area, S (cm^2)
24.7 ± 1.3	163.32 ± 24.98	238 ± 26

velocity of the propulsive wave, λ/t, where λ = length of the propulsive wave).

Lighthill (1971), Wardle and Reid (1977), and Videler (1981) have pointed out that the integral term in equation 6 approximates

$$(7)\quad \frac{d}{dt}\cdot(0.5\cdot m\cdot w\cdot z)_{a\,=\,0}.$$

Thus the important parameters affecting thrust are t, H, λ, and B. Furthermore the overall effect of a given form of body deformation on thrust can be summarized in terms of a trailing edge reference (Wu 1977):

$$(8)\quad T = K_T\cdot t^{-2}\cdot H^2\cdot B^2\cdot[1-u(t/\lambda)]$$

where each parameter applies to the caudal fin trialing edge ($a = 0$).

K_T is a proportionality constant that will vary with the body deformation pattern ranging from that seen in steady swimming to that of fast-starts. In steady swimming, mean thrust can be calculated as the average rate of convection of momentum to the wake at the trailing edge. This is called a bulk momentum simplification (Lighthill 1975; Wu 1977). For this bulk momentum situation, the mean value of K_T in equation 8 is $\pi^3/8$ (Wu 1977). For unsteady motions, K_T will take larger values, as the body anterior to the trailing edge will also contribute to thrust.

The null hypothesis that routine swimming is quasi-steady is not unreasonable because it is well known that speeds and acceleration rates are not large (Nursall 1958). If routine swimming is quasi-steady, then the bulk momentum form of the model will predict average thrust. In addition, H, B, λ, and t at various mean u in routine swimming should be comparable with values widely reported for fish swimming steadily in flumes.

Materials and Methods

Observations were made on rainbow trout, *Oncorhynchus mykiss* (formerly *Salmo gairdneri*). Morphological characteristics are summarized in Table 1.

Individual fish were filmed swimming in a covered tank, 200 cm in diameter and 15 cm deep. Fish were acclimated to the tank for 2 d before observation, during which time they were not fed. Water temperature was 15°C. Trout were usually stationary, but during voluntary swimming, trout swam continuously at low speed, sometimes around the periphery of the tank and sometimes over the whole tank area. During voluntary swimming, the observed ranges of swimming speeds, acceleration rates, and turning radii were commonly small, <25 cm·s^{-1}, ± 45 cm·s^{-2}, and <25 cm·s^{-2}, respectively. In order to provide a wider data range for analysis, swimming of each trout was also recorded in another tank 50 cm square and 10 cm deep while feeding on fathead minnow (*Pimephales promelas*) prey. The same acclimation and test conditions were used as for the larger tank. The resultant stalking and attacking movements of the foraging trout were recorded. Kinematic analysis focuses on these observations, and data were accumulated for all individuals.

Swimming movements were recorded on 2-cm videotape with a camera shutter speed of 1000 Hz to give sharp images. Portions of the tape were selected at random and played back field-by-field (60 Hz). The number of fields elapsed and the positions of the center of mass of the body and of the caudal fin trailing edge were recorded for every half tail-beat, measured from one lateral extreme of the tail to the next. The center of mass was assumed to be located at the midpoint of the body, one third of the body length from the nose (Webb 1978, 1982). Mean tail-beat period and speed, acceleration rate, and turning radius of the fish were determined for complete tail-beats comprising two successive half-beats. This is essentially a three-point moving regression technique, with the period, determined from the frame count for each half tail-beat, being the sum of periods for the two half-beats. Mean speed was the average of speeds calculated from the distance travelled along the mean path and the duration of each half-beat. The average acceleration was calculated from the differences in velocity for the successive half-beats. The turning radius was calculated by assuming that the three locations of the center of mass during two half tail-beats lay on a common circle. Then the center of the turning circle for these three locations was the point of intersection of perpendicular bisectors of the chords linking successive locations.

The method used in the analysis differentiates distance–time data to obtain velocity and acceleration. The method is notorious for oversmoothing highly unsteady motions. Errors occur because high framing rates are required for good temporal resolution of displacements. Successive locations of the center of mass or other landmark on the body then tend to be close together, but accuracy increases for spatial resolution when locations are widely spaced. Harper and Blake (1989) showed that certain errors for a given framing rate are minimized when time periods and distances travelled are large, such as is usual when average performance measures are determined. Similarly, error will be small when acceleration rates are small. These conditions pertain to the present study. Nevertheless, any high-frequency variations in speed, acceleration, and deceleration that might occur within half tail-beats would be smoothed out.

The shape of the centerline of the body was traced. The average length of the propulsive wave was measured for a tail-beat by superimposing these tracings and measuring the distance between nodes (Webb et al. 1984).

The composition of routine swimming was determined from 347 half tail-beats (226 full tail-beats) for 10 trout, covering a total of 2 min. Data were analyzed using TROLL (Anonymous 1979) and SYSTAT (Wilkinson 1987).

Results

During most tail-beats, fish usually accelerated, decelerated, and/or turned (Fig. 1). No successive tail-beats with similar average speeds were found for fish swimming in either the large or small tank.

Swimming speeds during routine swimming are well known to be skewed towards low values, and this was found here ($g_1 = 1.404$). Using foraging trout as an example (Fig. 2A), speeds ranged from 0.5 to 116 cm·s^{-1}. The median speed was only 14 cm·s^{-1} (0.5 L·s^{-1} where L is total length of the body).

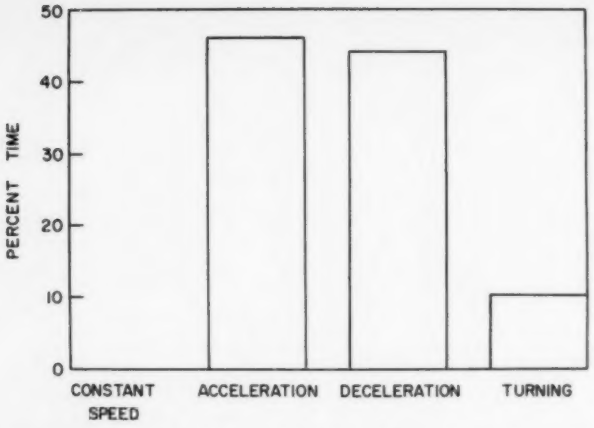

FIG. 1. Percentages of 226 complete tail-beats from 10 trout in which speed was constant (within ±5% of the mean of preceeding tail-beat), fish accelerated, decelerated, and turned during routine swimming.

The mean speed was 32 $cm \cdot s^{-1}$. Values of this order, about 1 $L \cdot s^{-1}$, are representative of average swimming speeds during routine swimming (Weihs and Webb 1983).

Skewed frequency distributions were also found for linear and centripetal acceleration (g_1 = 5.2 and 4.3, respectively). For foraging trout, small acceleration rates dominated routine swimming (Fig. 2B and 2C). Average accelerations were 114 $cm \cdot s^{-2}$ and average decelerations were -88 $cm \cdot s^{-2}$ (Fig. 2B). Centripetal acceleration rates had median and mean values of 31 and 104 $cm \cdot s^{-2}$ (Fig. 2C).

All these performance values are small compared with maxima reported in the literature. Maximum values of speed, linear acceleration rate, and centripetal acceleration rate would be expected to be about 340 $cm \cdot s^{-1}$, >5000 $cm \cdot s^{-2}$, and 4000 $cm \cdot s^{-2}$, respectively (Wardle 1975; Webb 1978).

Speed, not surprisingly, was correlated with both centripetal acceleration rate (u^2/r) and with acceleration rate, since changes in speed must follow acceleration or deceleration (Table 2). However, turning radius was not correlated with speed, as theorized by Howland (1974) and shown in laboratory studies by Webb (1983). As a result, the correlation between speed and centripetal acceleration was not particularly strong.

Trout tail-beat periods were skewed towards small values (Fig. 3A; g_1 = 1.408), with the average being 0.34 s and the median being 0.15 s. These tail-beat periods were larger than the minimum period possible of about 0.06 s (Wardle 1975).

Where motions repeat cyclically, as in steady swimming, tail-beat timing can be described in terms of tail-beat frequency or period. The former is usually reported in studies of steady swimming, while tail-beat period is the usual measure of timing for nonrepeating motions (e.g. Weihs and Webb 1983). To facilitate comparisons with data reported in the literature on steady swimming, tail-beat periods were recomputed as tail-beat frequencies, tbf, and related to specific swimming speed, u/L:

$$(9)\quad \text{tbf} = 0.98 \pm 0.31 + 2.54 \pm 0.023 \cdot u/L, \qquad r^2 = 0.676,\ p < 0.001.$$

Regression coefficients are shown ±2 SE.

Equation 9 differs from relationships obtained during steady swimming of trout in flumes. For example, Webb et al. (1984) obtained the following for trout over a wide range of sizes:

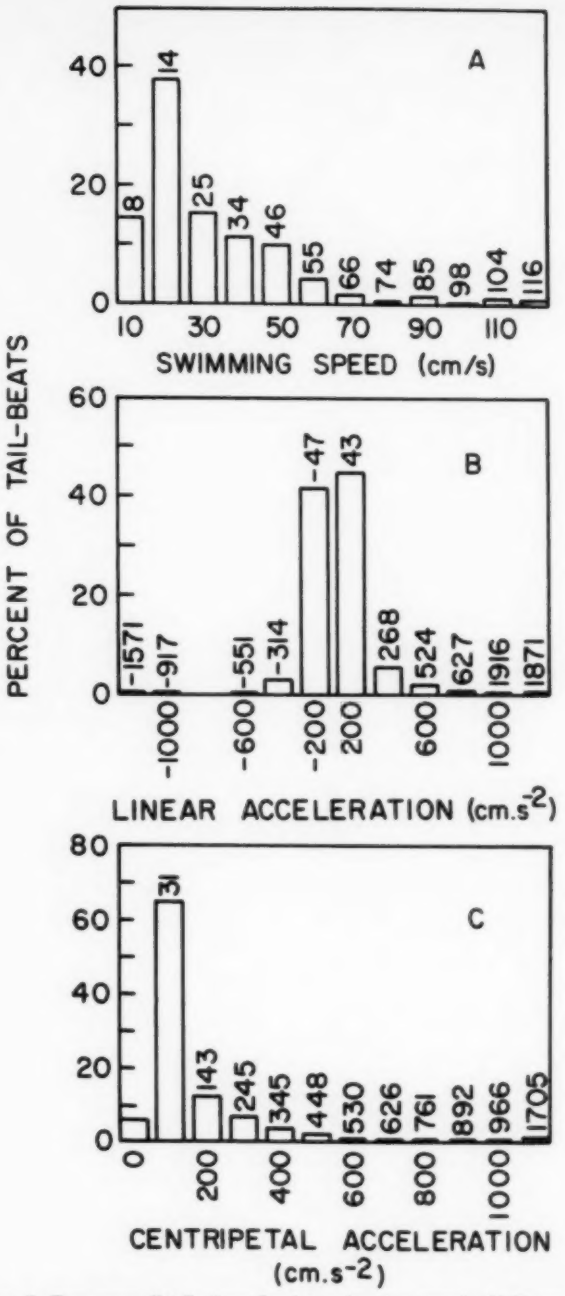

FIG. 2. Frequency distributions for (*a*) swimming speed, (*b*) linear acceleration rate, and (*c*) centripetal acceleration rate (u^2/r) during prey stalk, pursuit, and capture by rainbow trout. Averages for each bin are shown above each vertical block.

$$(10)\quad \text{tbf} = 3.19 \pm 0.19L^{-1/3} + 1.29 \pm 0.03 \cdot u/L.$$

The intercept for trout of the size studied here would be 1.09, which overlaps the 95% confidence limits for the intercept of equation 9. However, the slopes clearly differ so that tail-beat frequency in routine swimming increasingly diverged from that in steady swimming as average speed increased, i.e. at a given

TABLE 2. Pearson correlation matrix (two-tailed tests) for the kinematic factors affecting thrust and resistance for routine swimming during foraging by rainbow trout. a = average linear acceleration during a tail beat; H = trailing edge amplitude; λ = length of propulsive wave; u = average swimming speed during a tail-beat; r = turning radius. *** = $p < 0.001$; ** = $0.001 < p < 0.01$; * = $0.01 < p < 0.02$; ns = $p > 0.05$. Relationships between some variables were better described by a nonlinear model, resulting in significant correlations between t and a and u and a. These results are shown in parentheses.

	t	H	λ	u	a
H	0.13 ns				
λ	0.21*	0.06 ns			
u	−0.67***	−0.02 ns	−0.16		
a	(−0.49**)	−0.06 ns	0.07	(0.39**)	
u^2/r	−0.20*	0.03 ns	−0.06	0.20*	0.13 ns

average speed, fish work harder in routine swimming than at the same speed in steady swimming.

Trout tail-beat amplitudes were skewed ($g_1 = 0.78$) towards smaller values in the range observed (Fig. 3B). This is not unexpected, since routine swimming performance involved low levels of speed and acceleration. The average amplitude was 4.9 cm, or 0.2L. Amplitudes of fish swimming steadily in flumes are typically reported to average 20% of the total length (Webb 1975).

The median length of the propulsive wave (Fig. 3C) was 9 cm (0.8L) and the mean length was 22 cm (0.9L). These are typical for fish of the size used (Wardle 1975; Webb 1975).

Tail-beat amplitude (H) and period (t) and tail-beat amplitude and wavelength (λ) were not correlated (Table 2). However, tail-beat period was correlated with wavelength, although weakly. Tail-beat amplitude and the length of the propulsive wave were not significantly correlated with performance. Tail-beat period was correlated with speed, linear acceleration rate, and centripetal acceleration rate where speed squared is a major parameter (Table 2).

Data from Table 1 and Figs. 2 and 3 were used to determine expected thrust, drag, inertial resistance, centripetal resistance, and net resistance (Table 3). Since performance levels were small, forces were also small. On average, drag was smaller than acceleration resistance components, but all the resistance components of drag, linear acceleration resistance, and centripetal acceleration resistance were of similar magnitude.

Thrust, T, is equal to net resistance, R, so that

$$(11) \quad T = K_1 \cdot R$$

and K_1 should be unity. However, T averaged 0.092 N and R averaged 0.14 N (Table 3), and the difference was significant (t-test, $p < 0.001$). In addition, T and R were compared in a functional regression (since there is no true independent variable):

$$(12) \quad T = 0.422 \pm 0.064 \cdot R, \qquad r^2 = 0.436,\ p < 0.001,\ n = 226.$$

The regression coefficient is significantly different from unity. Resistance cannot be smaller than the minimum calculated using equations 1 to 4. Therefore, resistance is underestimated and/or both thrust and resistance are underestimated in this analysis. Therefore, one or more of the assumptions are in error so that routine swimming is not quasi-steady and/or resistance components do interact.

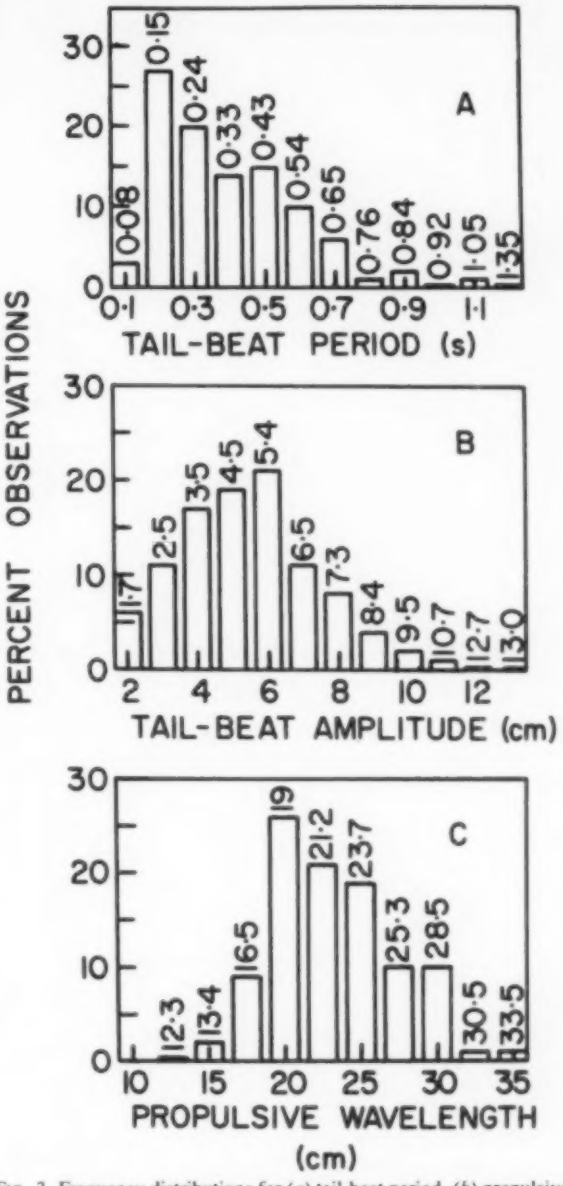

FIG. 3. Frequency distributions for (*a*) tail-beat period, (*b*) propulsive amplitude, and (*c*) tail-beat wavelength during prey stalk, pursuit, and capture by rainbow trout. Averages for each bin are shown above each vertical block.

Similarly, equation 5 can be written as

$$(13) \quad T = R = \sqrt{[(a_1 \cdot R_{drag} + a_2 \cdot R_{linear})^2 + a_3 \cdot R^2_{centripetal}]}$$

and these regression coefficients are also expected to be unity and equal. However,

$$(14) \quad T = \sqrt{[2.83 \pm 0.48 \cdot R_{drag} + 0.22 \pm 0.010 \cdot R_{linear})^2 + 0.16 \pm 0.014 R_{centripetal}]}$$

and $p < 0.001$ for a_1 and a_2 and $p < 0.05$ for a_3. Again, the regression coefficients differ from unity, suggesting that resistance and/or thrust and resistance are underestimated.

TABLE 3. Summary of mean and range for thrust, assuming that routine swimming is quasi-steady, and resistance components, assuming no resistance interactions for rainbow trout. Means were obtained after log-transformation to improve normality of the data. All units are Newtons.

	Lower range limit	Upper range limit	Log mean ± 2 SE	Mean
Thrust, T (equation 8)	2.0×10^{-3}	1.67	−1.00 ± 0.083	0.092
Net resistance, R (equation 5)	4.0×10^{-3}	3.12	−0.86 ± 0.077	0.14
Drag, R_{drag} (equation 1)	3.7×10^{-6}	0.35	−1.63 ± 0.023	0.023
Linear acceleration resistance, R_{linear} (equation 3)	2.3×10^{-4}	1.93	−0.87 ± 1.10	0.13
Linear deceleration resistance, R_{linear} (equation 3)	2.0×10^{-4}	−1.79	−(−1.24 ± 0.15)	−0.057
Centripetal resistance, $R_{centripetal}$ (equation 4)	6.0×10^{-6}	3.09	−1.36 ± 0.13	0.043

Discussion

The data on tail-beat frequency (equations 9 and 10) show unequivocally that fish work harder at a given average speed in routine swimming than at the same speed in steady swimming. This might be due to the additional resistance components associated with accelerations, correctly calculated by the bulk momentum model.

In practice, calculations of thrust in routine swimming using the bulk momentum model estimate the *minimum* possible thrust. Numerous studies have shown interrelationships among swimming speed, kinematics, metabolic rate, and mechanical rate of working during steady swimming. These show that a given body deformation at any steady swimming speed generates a known thrust (equal to drag) and expends energy at a known rate. When there are deviations from these regular repeating motions, the body anterior to the trailing edge contributes to mean thrust, increasing the magnitudes of the forces produced (Weihs 1972, 1973; Wardle and Reid 1977; Videler 1981).

If contributions of the anterior of the body to thrust occur, but are neglected, then the bulk momentum assumption will underestimate thrust. Under these circumstances, the coefficient K_1 in equation 12 would be less than unity, as observed (equation 13). In addition, since unsteady motions are associated with thrust from the anterior of the body, then the coefficients a_2 and a_3 associated with accelerations in equation 13 would be less than unity, again as observed (equation 14).

Therefore, solutions to equations 11 and 13 (equations 12 and 14) suggest that the body anterior to the trailing edge makes significant contributions to instantaneous and mean thrust, such that the bulk momentum model does not accurately predict thrust. As a result, routine swimming is not quasi-steady.

This conclusion implies that thrust and rates of working in routine swimming can only be determined from detailed knowledge of the entire motion of the fish body. Such a task is formidable in the laboratory and is essentially impossible for free-swimming fish. However, there are two additional consequences arising from the solutions to equations 11 and 13 that suggest a practical alternative. First, drag may be increased. Second, drag dominates net resistance.

TABLE 4. Percentage average changes in calculated net resistance using original coefficients in equation 13, $T = R = \sqrt{[(a_1 \cdot R_{drag} + a_2 \cdot R_{linear})^2 + a_3 \cdot R^2_{centripetal}]}$, after their replacement with the values shown in the table. Net resistance was calculated for the entire data set for combinations of the coefficients given in the Table and the average determined.

a_1	a_2	a_3	% change in thrust
2.83	0	0.16	1
2.83	0.22	0	−2
2.83	0	0	−1
	10% changes in a_1		
1.1 × 2.83	0.22	0.16	−10
0.9 × 2.83	0.22	0.16	−10

Net resistance is assumed to be the vector sum of noninteracting components associated with speed and accelerations (Weihs 1981). If there are no interactions among components (or interactions affect each component equally), then the regression coefficients a_1, a_2, and a_3 in equation 13 should be equal, since resistance components and thrust are presumed to be correctly computed using equations 1, 2, 4, and 8. Regression coefficients are not found to be equal (equation 14). In addition, $a_1 >> 1$, which suggests that the propulsor must work very much harder to overcome drag than would be expected.

The apparent increase in drag dominates the force balance. The coefficient a_1 is over an order of magnitude larger than a_2 and a_3. The impact of the large differences in regression coefficients is amplified because the squares of the resistance components contribute to net resistance (equation 13). As a result, although the theoretical linear and centripetal resistance components are of the same order of magnitude as the theoretical drag (Table 3), these acceleration resistance components contribute little to net resistance. The regression coefficients for

equation 14 were modified in various ways (Table 4) and their average impact determined on thrust as predicted by equation 14 for the whole data set. The effect of reducing a_2 and/or a_3 to zero was negligible. In contrast, 10% changes in a_1, and hence the drag contribution to net resistance, resulted in 10% changes in thrust.

Although routine swimming is not quasi-steady, the drag term dominates routine swimming *just as it appears to in steady swimming*. Therefore, thrust and rates of working in routine swimming might be estimated from coveniently measured kinematic variables or average speed, *as if routine swimming were quasi-steady* and assuming drag is elevated by a factor of approximately 3, the value of a_1. It should be noted that this correction factor is additional to k (equation 1) to account for self-propulsion of a flexing body.

Other studies suggest that rates of working are increased by a factor of the same order as that indicated here. Videler (1981) calculated the total thrust during an acceleration by Atlantic cod, *Gadus morhua*. It can be determined from his data that drag was increased by a factor of 3.4, this being additional to resistance associated with inertia of the body. Brett (1973) measured the metabolic rate of a group of sockeye salmon, *Oncorhynchus nerka*, swimming in a water tunnel. During periods of aggression, metabolism was elevated by a factor of about 2, although average speed was unchanged. Agonistic behaviors typically involve maneuvers (Keenleyside 1979), although these were not quantified in Brett's study. Weatherley et al. (1982) and Weatherley and Gill (1987) have shown that metabolic rate in routine swimming is increased by a factor of about 4 compared with that measured at the same average speed during steady swimming. Puckett and Dill (1984) found that the rate of oxygen consumption of coho salmon, *Oncorhynchus kisutch*, accelerating to strike food was elevated by a factor of 5 to 20 compared with rates expected at steady swimming speeds equal to the average strike speeds. These latter results are very variable because they were based on "oxygen debt." They may also be high because efficiency is greater at higher swimming speeds (see Webb 1975), and this was not taken into consideration.

The studies discussed above have been performed in laboratories, and the results are assumed to have external validity. This may not be correct. For example, the present study considers motion in only one plane whereas complete description of the motion of an aquatic vertebrate in space is defined by the state and control variables for three orthogonal planes. In practice, vertebrate motions usually can be described in two dimensions. Most fish occupy a relatively limited horizontal plane, as imposed in the present experiments. Buoyancy regulation using gas inclusions often limits vertical depth because of the effect of pressure on gas volume, following Boyle's law, and hence specific gravity (see Alexander 1967; Lagler et al. 1977). Benthic animals and those living close to the air–water surface also tend to swim routinely over a restricted depth range (Bone and Marshall 1982). Vertebrates are highly flexible in one direction and large translations tend to occur in that plane. When vertical movements are large, such as for myctophids or cetaceans, the vertical excursions can probably be approximated to a plane, in this case largely oriented vertically.

In addition, walls may have forced more turns and accelerations than in the field. In practice, frequent turns are expected during routine swimming, for example in searches, staying in food patches, maneuvering among structures such as weeds or corals, etc.; acceleration maneuvers are an integral part of prey capture and predator avoidance. These acceleration-based behaviors are readily seen in natural habitats, such as among inshore schooling fish, stream communities, etc. Such observations show that linear and centripetal acceleration are common features of normal behavior, and it seems likely that these behaviors affect rates of working in the field in the same way as in the laboratory.

There are undoubtedly some situations where this conclusion is wrong and constant-speed swimming dominates routine swimming. Examples might include some pelagic fish and cetaceans, and lotic fish holding station in a current. Thus, large selachians, tunas, and also smaller scombrids appear to swim regularly and continuously at low speeds (e.g. Thomson and Simanek 1977; Sharp and Pirages 1978; Weihs et al. 1981). Feldmeth and Jenkins (1973) and Feldmeth (1983) described similar swimming by trout in a stream, which was sufficiently regular that energy expenditures could be estimated from correlations with tail-beat frequency. Nevertheless, swimming at uniform speed is probably the exception rather than the rule.

Finally, analysis of routine swimming kinematics has potential for a wide range of studies on swimming functional morphology. Many organisms, such as cetaceans, elasmobranchs, thunnids, and fish larvae, are difficult to test using standard methods because of their size and/or delicacy. With models such as those described here, correlations among various aspects of general swimming kinematics and performance may be compared for routine activities of animals in large tanks, pools, and in the field.

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Analysis of Length Frequency Samples with Relative Abundance Data for the Gulf of Maine Northern Shrimp (*Pandalus borealis*) by the MULTIFAN Method

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We present an extension of the MULTIFAN method for simultaneously analyzing several length frequency data sets from length frequency data collected by research trawl surveys. The assumption that the research trawl samples the animals in a regular fashion allows the proportions at age in the samples to be parameterized in terms of relative year class strengths and the age-dependent selectivity of the sampling procedure. When available, relative abundance data can be incorporated into the analysis and permit the estimation of mortality. The method is applied to Gulf of Maine northern shrimp (*Pandalus borealis*) data.The parameter estimates obtained agree substantially with those previously obtained using a more detailed knowledge of the species' biology.

On présente une augmentation de la méthode MULTIFAN pour l'analyse simultanée de plusieurs séries de données sur la fréquence des longueurs par rapport aux données sur la fréquence des longueurs recueillies au cours de relevés expérimentaux par chalutage. L'hypothèse selon laquelle le chalut expérimental échantillonne les animaux selon un régime régulier signifie que les proportions selon l'âge dans les échantillons peuvent être paramétrées en termes de l'abondance relative des classes et la sélectivité liée à l'âge de la méthode d'échantillonnage. Les données sur l'abondance relative, si disponibles, peuvent être incluses dans l'analyse pour déterminer le taux de mortalité. La méthode est appliquée à des données sur la crevette nordique (*Pandalus borealis*) du golfe du Maine. Les estimations des paramètres ainsi obtenues concordent étroitement avec celles obtenues auparavant à partir de données plus détaillées sur la biologie de l'espèce.

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The MULTIFAN system of length frequency analysis was introduced in Fournier et al. (1990) where it was applied to length frequency data from southern bluefin (*Thunnus maccoyii*), a slow-growing, relatively long-lived species. MULTIFAN is a robust likelihood-based method which simultaneously analyzes multiple length frequency data sets. The extra information made available by simultaneously analyzing multiple length frequency data sets combined with the use of a robust likelihood-based estimation procedure enables the model to perform hypothesis tests to distinguish between different models for fitting the data. In particular, it is possible to estimate the number of significant age classes which are present in the data.

While the model employed in Fournier et al. (1990) makes many assumptions about the distribution of the length at age of the animals, no assumptions are made about the process which gives rise to the proportions at age of the animals which make up the length frequency data sets. Allowing the proportions at age to be independent parameters produces a model formulation which is broadly applicable. However, introducing extra restrictions on the process which produces the proportions at age can lead to a model formulation with fewer parameters. Such a model can produce superior estimates of the parameters of interest so long as the extra assumptions are valid. An appropriate situation may arise in the analysis of research vessel trawl survey data.

A research vessel trawl survey can be designed so that the animals in each age class have the same relative probabilities of being captured in each year; thus the mean number per tow provides an index of relative abundance. If, in addition, it is assumed that all cohorts experience the same age-independent total mortality, it follows that the proportions at age in the samples and the relative abundance can be parameterized in terms of the relative year class strengths of the age cohorts, the total instantaneous mortality rate, and the age-dependent selectivity of the trawl gear. Such a parameterization is particularly useful if there is a large variation in year class strength so that the model can "follow" the strong and weak year classes over time through the data sets.

To illustrate the application of MULTIFAN to research vessel trawl survey length frequency data whch satisfy these assumptions, we have chosen a 6-yr time series of trawl survey catch data for Gulf of Maine northern shrimp (*Pandalus borealis*) for the years 1984–89. These data and a priori assumptions about the parameters used in our analysis are summarized in Terceiro and Idoine (1989) and in survey cruise

reports from the Northern Shrimp Technical Committee (NSTC 1989).

Length Frequency Data

Gulf of Maine Northern shrimp are protandric hermaphrodites, with the females the target of a valuable winter–spring otter trawl and pot fishery in the western Gulf of Maine. A stratified random research trawl survey, conducted annually during late July through mid-August aboard the Northeast Fisheries Center (NEFC) R/V *Gloria Michelle* in the western Gulf of Maine, was implemented in 1983 to provide a fisheries-independent source of data for the stock. Data from identical sample strata sets are available for 1984–89 (NSTC 1984, 1985, 1986, 1987, 1988, 1989). To date, abundance and biomass indices from the R/V *Gloria Michelle* survey (stratified mean number per tow, stratified mean weight (kilograms per tow) have proven to be accurate predictors of commercial fishery performance (total catch and catch per unit effort; NSTC 1988).

Information is available from previous analyses of length frequency distributions from the Gulf of Maine shrimp survey to provide a baseline interpretation for evaluation of MULTIFAN results. The Gulf of Maine stock is assumed to be one of the shortest lived of the North Atlantic pandalid shrimps. The von Bertalanffy growth equation is the accepted means of modeling the growth of *P. borealis* (Frechette and Parsons 1983). Four age groups (ages 1–4) are usually present in the trawl survey catches (McInnes 1986), with a maximum age of 5 yr (Haynes and Wigley 1969), based on modes in length frequencies and sexual characteristics (Allen 1959; McCrary 1971). Gulf of Maine northern shrimp in a length range of 13–18 mm mean carapace length (CL) are generally assumed to be of age group 1, and mainly immature and mature males, while shrimp of 18–22 mm CL are assumed to be of age group 2, and mostly mature males. Animals in the 22–25 mm CL interval are assumed to be of age group 3, usually females with no previous spawning history. Shrimp larger than 25 mm CL are assumed to be females of age group 4, with possible age group 5 female shrimp at CL greater than 29 mm. The survey samples northern shrimp in a CL range of 10–33 mm, with animals assumed to be fully recruited to the gear at about 19–20 mm CL, or age group 2 and older (Blott et al. 1983). Survey results and commercial fishery performance suggest that the 1982 and 1987 year classes of Gulf of Maine northern shrimp were strong, and the 1983 year class very weak, with the remaining cohorts (1984–86, 1988) of about equally mediocre strength (NSTC 1987, 1988, 1989). Previous work has also suggested that the large 1982 year class experienced a slower than average growth rate (Terceiro and Idoine 1989).

Model Formulation

The following notation is introduced to describe the MULTIFAN model:

i	subscript indexing the length frequency intervals.
j	subscript indexing the age classes.
α	subscript indexing the length frequency data sets. To simplify the discussion it is also used to index the year the sample was taken. This uses the fact that for these data there is exactly one sample per year.
N_J	number of age classes present in the data sets.
N_A	number of length frequency data sets.
N_I	number of length intervals in each length frequency data set.
S_α	number of shrimp in the αth length frequency data set.
$f_{i\alpha}$	number of shrimp whose lengths lie in the ith length interval in the αth length frequency data set.
$p_{j\alpha}$	proportion of age class j shrimp in the αth length frequency data set.
$q_{ij\alpha}$	probability that an age class j shrimp picked at random from those sampled to get the αth length frequency data set has a length lying in length interval i.
$Q_{i\alpha}$	probability that a shrimp picked at random from those in the αth length frequency data set has a length lying in length interval i.
$\tilde{Q}_{i\alpha}$	proportion of shrimp in the αth length frequency data set having a length lying in length interval i.
$\mu_{j\alpha}$	mean length of the age class j shrimp in the αth length frequency data set.
$\sigma_{j\alpha}$	standard deviation of the length distribution of the age class j shrimp in the αth length frequency data set.
χ_i	midpoint of the ith length frequency interval.
w	width of the length frequency intervals.
L_1	mean length of the first age class on the von Bertalanffy curve.
L_{N_J}	mean length of the last age class on the von Bertalanffy curve.
K	von Bertalanffy K parameter.
ρ	Brody growth coefficient ($K = -\log_{e(\rho)}$).
λ_1, λ_2	parameters determining the standard deviations $\sigma_{j\alpha}$.
τ_α	parameters determining the overall variance of the sampling errors in the αth length frequency data set.
$\xi_{i\alpha}$	parameters determining the relative variances of the sampling errors within the αth length frequency data set.
δ	parameter determining the variance of the sampling errors in all the length frequency data sets.
$N_{j\alpha}$	relative number of age class j shrimp in the population at the time when the αth length frequency data set was gathered.
Z	instantaneous total mortality rate.
s_j	selectivity coefficients for the trawl survey.
C_α	total research trawl catch for the αth length frequency data set.
E_α	sampling effort used to collect the αth length frequency data set.
q	catchability coefficient for the trawl survey.
ϵ_α	random variables determining the variation in the catch – estimated fishing effort relationship.
σ_E	variance of the random variables ϵ_α in the catch – estimated fishing effort relationship.
ϵ_i	random variables determining the variation in the relationship between the relative abundance index and the total relative population size in year i.
$\mathcal{L}$	log-likelihood function.

Robust Estimation

MULTIFAN employs a robust maximum likelihood estimation procedure. The motivation for using this procedure and the technical aspects of the procedure are described in Fournier et al. (1990). We shall not repeat this discussion here, but for convenient reference we briefly describe the form of the log-likelihood function employed.

If the $\hat{Q}_{i\alpha}$ are derived from a random sample of size S_α, they would be random variables with means $Q_{i\alpha}$ and variances $(1 - Q_{i\alpha})\, Q_{i\alpha}/S_\alpha$. Set $\xi_{i\alpha} = (1 - Q_{i\alpha})\, Q_{i\alpha}$. The $\xi_{i\alpha}$ determine the relative variances of the $\hat{Q}_{i\alpha}$ within a sample while the S_α can be regarded as a scale factor determining the overall size of all the variances of $\hat{Q}_{i\alpha}$ in a sample. The scale factor S_α is replaced by a parameter τ_α to be estimated within the model.

We assume that the variance of the random variable $\hat{Q}_{i\alpha}$ is equal to $(\xi_{i\alpha} + 0.1/N_l)\tau_\alpha^2$ where, as above, the τ_α are parameters to be estimated.

As mentioned in Fournier et al. (1990), the term $0.1/N_l$ is included in the variance calculation to ensure that the variance associated with the random variable $\hat{Q}_{i\alpha}$ does not approach 0 as the expected value $Q_{i\alpha}$ approaches 0. The question is "What is small for the expected proportion of observations which lie in a given length frequency interval?" Since there are N_l length frequency intervals, the average proportion of observations in any length frequency interval is $1/N_l$. For a small expected proportion, we have picked 1/10 of this value which is $0.1/N_l$.

The likelihood function employed in the MULTIFAN model is

$$(1.1)\quad \prod_{\alpha=1}^{N_A}\prod_{i=1}^{N_l}\left[\frac{1}{\sqrt{2\pi\xi_{i\alpha}+0.1/N_l)}\,\tau_\alpha}\times\left(\exp\left\{-\frac{(\hat{Q}_{i\alpha}-Q_{i\alpha})^2}{2(\xi_{i\alpha}+0.1/N_l)\,\tau_\alpha^2}\right\}+0.01\right)\right]$$

Taking the logarithm of (1.1) we obtain the log-likelihood function $\mathcal{L}$:

$$(1.2)\quad \mathcal{L} = -1/2\sum_{\alpha=1}^{N_A}\sum_{i=1}^{N_l}\log_e(2\pi(\xi_{i\alpha}+0.1/N_l)) - \sum_{\alpha=1}^{N_A} N_l\log_e(\tau_\alpha) + \sum_{\alpha=1}^{N_A}\sum_{i=1}^{N_l}\log_e\left[\exp\left\{\frac{-(\hat{Q}_{i\alpha}-Q_\alpha)^2}{2(\xi_{i\alpha}+0.1/N_l)\tau_\alpha^2}\right\} + 0.01\right].$$

Let δ be a model parameter which determines the overall size of the variances in the sampling errors. The assumption that all samples are equally accurate is implemented by setting $\tau_\alpha = \delta$ for all α. Expression (1.2) forms the basis for the robust likelihood-based estimation scheme we have adopted, that is, the parameters are estimated by maximizing expression (1.2).

Main Assumptions of the Model

Most of the model structure involves some biological assumptions which are made to reduce the number of independent parameters. The main structural assumptions are as follows:

(1) The lengths of the shrimp in each age class are normally distributed around their mean length (see(2.1)).

(2) The mean lengths at age lie on a von Bertalanffy growth curve (see(2.3)).

(3) The standard deviations of the actual lengths about the mean length at age are a simple function of the mean length at age (see (2.4)).

(4) The proportions at age of the shrimp in the length frequencies arise from a biased (because of partial selection by the sampling gear) random sample of the shrimp where the bias is the same for each year.

If the lengths of the age class j shrimp in the αth length frequency data set are normally distributed around their mean $\mu_{j\alpha}$ with standard deviations $\sigma_{j\alpha}$, the $q_{ij\alpha}$ can be expressed in terms of $\mu_{j\alpha}$ and $\sigma_{j\alpha}$ by

$$(2.1)\quad q_{ij\alpha}(\mu_{j\alpha},\sigma_{j\alpha}) = \frac{1}{\sqrt{2\pi}\,\sigma_{j\alpha}}\int_{x_i-w/2}^{x_i+w/2}\exp\left\{\frac{-(x-\mu_{j\alpha})^2}{2\sigma_{j\alpha}^2}\right\}dx.$$

As long as $\sigma_{j\alpha} > w$ the integral can be approximated sufficiently well by setting

$$(2.2)\quad q_{ij\alpha}(\mu_{j\alpha},\sigma_{j\alpha}) = \frac{w}{\sqrt{2\pi}\,\sigma_{j\alpha}}\exp\left\{\frac{-(x_i-\mu_{j\alpha})^2}{2\sigma_{j\alpha}^2}\right\}.$$

This approximation has been used in the model.
If the mean lengths $\mu_{j\alpha}$ lie on a von Bertalanffy curve, then

$$(2.3)\quad \mu_{j\alpha} = L_1 + (L_{N_l} - L_1)\left[\frac{1-\rho^{j-1}}{1-\rho^{N_l-1}}\right]$$

where L_1, the mean length of the first age class, L_{N_l}, the mean length of the last age class and ρ, the Brody growth coefficient, are the three parameters which determine the form of the von Bertalanffy curve. This parameterization of the von Bertalanffy growth curve is from Schnute and Fournier (1980).

The standard deviations $\sigma_{j\alpha}$ are parameterized as a simple function of length involving two parameters, λ_1 and λ_2:

$$(2.4)\quad \sigma_{j\alpha} = \lambda_1\exp\left\{\lambda_2\left[-1+2\left(\frac{1-\rho^{j-1}}{1-\rho^{N_l-1}}\right)\right]\right\}$$

where the term enclosed in square brackets expresses the length dependency of the standard deviations independently of the numerical values of the parameters L_1 and L_{N_l} (cf.(2.3)). The two coefficients, λ_1 and λ_2, transform the rescaled length to the standard deviations. The coefficient λ_1 determines the magnitude of the standard deviations, and λ_2 determines the length dependent trend in the standard deviations. If $\lambda_2 = 0$, the standard deviations are length independent.

Parameterizing the Proportions at Age

The major difference between the present model and that of Fournier et al. (1990) is the different parameterization of the proportions at age. In the latter paper the proportions at age, $p_{j\alpha}$, are independent model parameters. In the present paper the proportions at age are presumed to arise from more or less regular sampling of an age-structured population and to reflect the underlying year class strength and, if present, the age-selective bias of the sampling procedure. To motivate our parameterization of the proportions at age, it is useful to consider which parameters might be estimable, given a collection of trawl survey length frequency data.

Let $N_{j\alpha}$ denote the number of age class j shrimp in the population in year α. We shall assume that the proportions at age of the shrimp in the length frequency samples satisfy the relationship

$$(3.1)\quad p_{j\alpha} = \frac{s_j N_{j\alpha}}{\sum_{r=1}^{N_J} s_r N_{r\alpha}}$$

where the selectivities s_j are assumed to satisfy the relationship

$$(3.2)\quad 0 < s_1 \leq s_2 \leq \ldots \leq s_{N_J} = 1.$$

The relationship (3.2) reflects the assumption that the shrimp "recruit" to the trawl gear. Setting $s_{N_J} = 1$ normalizes the parameterization of the selectivities. It ensures that the s_j can be interpreted as the ratio of the probability that an age class j shrimp will be captured by the trawl gear to the probability that an age class N_j shrimp will be captured by the trawl gear.

Let $C_{j\alpha}$ be the total research trawl catch of age j shrimp in year α. We shall assume that

$$(3.3)\quad \sum_{j=1}^{N_J} C_{j\alpha} = \sum_{j=1}^{N_J} q s_j N_{j\alpha} E_\alpha e^{\epsilon_\alpha}$$

where E_α is some measure of fishing effort and the ϵ_α are independent normally distributed random variables with variance σ_E^2. Define the observed catch per unit effort U_α by

$$(3.4)\quad U_\alpha = \sum_{j=1}^{N_J} C_{j\alpha}/E_\alpha$$

and T_α, the selectivity-weighted total number of shrimp in the population year α, by

$$(3.5)\quad T_\alpha = \sum_j s_j N_{j\alpha}.$$

Then equations (3.3), (3.4), and (3.5) imply that

$$(3.6)\quad \ln(U_\alpha) = \ln(q) + \ln(T_\alpha) + \epsilon_\alpha.$$

How well are the $N_{j\alpha}$ determined by the relationships (3.1)–(3.6)? Assume that values for the quantities $p_{j\alpha}$, s_j, $C_{j\alpha}$, E_α, and ϵ_α are fixed and that values of $N_{j\alpha}$ and q are found so that (3.1) – (3.6) are satisfied.

If all the $N_{j\alpha}$ are multiplied by the same constant u, the relationship (3.1) is unaltered. Relationships (3.3) and (3.6) also remain true if the parameter q is replaced by q/u. Thus the $N_{j\alpha}$ are determined at best only up to the constant u. This is not surprising. It simply means that the absolute size of the population cannot be determined from the proportions at age and the relative abundance.

Since the $N_{j\alpha}$ are not well determined, we pick a unique set of $N_{j\alpha}$ which we will refer to by $R_{j\alpha}$ by requiring that

$$\prod_{j=1}^{N_J} R_{j1} = 1.$$

A simple way of doing this is to set

$$(3.7)\quad R_{N_J 1} = \frac{1}{\prod_{j=1}^{N_J} R_{j1}}.$$

To complete the description of the relative cohort strength, we need the parameters $R_{1\alpha}$ where $2 \leq \alpha \leq N_A$.

Let Z denote the instantaneous total mortality rate. Assuming that all cohorts experience the same instantaneous total mortality rate, Z, the remaining relative numbers at age can be calculated from the relationship

$$(3.8)\quad R_{j+1,\alpha+1} = \exp(-Z) R_{j\alpha}$$

for $1 \leq j \leq N_J$ and $1 \leq \alpha < N_A$.

How well is the instantaneous mortality rate determined by relationships (3.1) – (3.6) and (3.8)? If Z is replaced by $Z + \psi$, the relative numbers of shrimp in year 2, R_{j2}, will be replaced by $R_{j2}e^{-\psi}$ for $2 \leq j \leq N_J$. Replacing R_{12} by $R_{12}e^{-\psi}$ will leave the relationship (3.1) unchanged. Continuing this way for the remaining years, we see that if $R_{1\alpha}$ is replaced by $R_{1\alpha}e^{-(\alpha-1)\psi}$ for $2 \leq \alpha \leq N_A$, then the relationship (3.1) will be left unchanged. This means that in the absence of relative abundance data as in equation (3.6), the instantaneous total mortality rate Z is completely undetermined because it is confounded with the trend in the size of the recruitment. It follows that in order to determine the instantaneous total mortality, it is necessary to have relative abundance data, or to make some additional assumption about the trend in recruitment. For example, if there were no relative abundance data, but it seemed reasonable to assume that there was no trend in abundance, it could be assumed that the relative abundance was the same for each year.

Equation (3.8) implies that there are no age class $N_j + 1$ shrimp in the population, that is the shrimp experience an instantaneous total mortality rate of Z in each year until they reach age class N_J when they simply die off at the end of the year. This model formulation will be referred to as model 1.

An alternative formulation (model 2) is obtained by assuming that the last "age class" consists of all animals of age N_J or older. This is done by modifying equation (3.8) for the last age class to

$$(3.9)\quad R_{N_J,\alpha+1} = \exp(-Z)\,(R_{N_J-1,\alpha} + R_{N_J\alpha}).$$

Models 1 and 2 represent two extreme ways of viewing the biology of the shrimp. For model 1 the shrimp keep growing on the von Bertalanffy curve for a certain number of years after which they all die out. For model 2 the shrimp grow for a certain number of years, after which they essentially stop growing, but live on indefinitely subject to the instantaneous total mortality rate Z. As usual, reality probably lies somewhere in between these two points of view.

Model 2 has an advantage over model 1 in that it is now necessary to decide how many age classes are in the data. Determining the exact number of age classes is problematic with older animals when the size at age no longer distinguishes age classes. Grouping older age classes in this situation (forming a "plus group") is analogous to the advantages obtained by grouping older age classes in catch at age models (Fournier and Archibald 1982).

Including Relative Abundance Data into the Model

Let A_i be the value of a relative abundance index in year i. We assume that

$$(3.10)\quad \ln(A_i) = \ln\left(\sum_{j=1}^{N_J} R_{ji}\right) + \epsilon_i$$

where the ϵ_i are independent normally distributed random variables. To implement this assumption into the estimation procedure, the quantity

$$(3.11)\quad p \sum_{i=1}^{N_A} \left(\ln(A_i) - \ln\left(\sum_{j=1}^{N_J} R_{ji}\right)\right)^2$$

is subtracted from the log-likelihood function (1.2). The term

p in expression (3.11) is a penalty weight which was set equal to 10.0 in the analysis. This corresponds to an assumption that the random errors ϵ_i in the relationship between the true relative abundance and the observed relative abundance have a variance of 0.05.

It is impossible to determine the "correct" value of the term p from the data alone. Using a value of 0 for p is equivalent to assuming that the catch per unit effort data have no information in them, that is not using them at all. Using a value of ∞ (a very large value such as 10^6 will suffice) for p is equivalent to assuming that the catch per unit effort index is a perfect indicator of relative abundance. The value of 10 used for p is a compromise between these two extremes. Usually in this type of analysis the answer obtained is not strongly dependent on the exact value of p employed. The analysis in this paper was repeated for values of p of 2 and 50. The results were almost identical to the ones presented here. The same model fits were selected as the "best" fits. The only differences were insignificant changes in the values of the parameter estimates obtained.

Calculating the Log-Likelihood Function

To implement the model, it is necessary to calculate the log-likelihood function $\mathcal{L}$ in expression (1.2). To carry out the calculation, we pick a set of fundamental parameters in terms of which all the model parameters can be calculated.

The parameters R_{j1} $(1 \leq j \leq N_J)$, $R_{1\alpha}$ $(2 \leq \alpha < N_A)$, Z, s_j $(1 \leq j \leq N_J)$, L_1, L_{N_J}, K, λ_1, λ_2, and δ form the fundamental set of parameters in terms of which the log-likelihood function (1.2) can be calculated. (If the relative accuracies of the length frequency data set are to be estimated, then the τ_α are independent model parameters instead of δ.) Note that the $Q_{i\alpha}$ satisfy the relationship

$$(4.1) \quad Q_{i\alpha} = \sum_{j=1}^{N_J} p_{j\alpha} q_{ij\alpha}.$$

The steps in the calculation of the model parameters are as follows:

(1) Calculate the $R_{j\alpha}$ from (3.8).

(2) Calculate the $p_{j\alpha}$ from (3.1) (recall that the $N_{j\alpha}$ are now given by the $R_{j\alpha}$).

(3) Calculate the $\sigma_j\alpha$ from (2.4) (recall that $\rho = \exp(-K)$).

(4) Calculate the $\mu_{j\alpha}$ from (2.3).

(5) Calculate the $q_{ij\alpha}$ from (2.2).

(6) Calculate the $Q_{i\alpha}$ from (4.1).

(7) Calculate the log-likelihood function $\mathcal{L}$ from (1.2).

Hypothesis Testing

The problem of choosing from all the possible fits to the data the one which "best" describes the process is dealt with by the theory of hypothesis testing. The importance of hypothesis tests in the analysis of length frequency data cannot be overemphasized. As in linear statistical models, we begin with a simple model and progress to more complicated model hypotheses involving more parameters. As an example, consider the selectivities s_j. We begin by assuming that all s_j are equal to 1 so that there is no age-dependent selectivity. We then test the hypothesis that $s_1 < 1$. If this hypothesis is accepted, we can test the hypothesis that $s_2 < 1$ as well. As another example, consider the standard deviations given by equation (2.4). We begin by assuming that $\lambda_2 = 0$ so that the standard deviations for all age classes are the same (length-independent standard deviations). We then introduce length-dependent standard deviations by allowing λ_2 to vary and test the hypothesis that $\lambda_2 \neq 0$.

In each case the question to be answered is whether a more complicated model (one with more parameters) should be accepted instead of a simpler model. The hypothesis test is carried out in the following way.

Let $\mathcal{L}_0$ and $\mathcal{L}_1$ be the value of the log-likelihood function for the simpler model and more complicated model. If the more complicated model provides a better fit to the data, then $\mathcal{L}_0 < \mathcal{L}_1$. The question to be answered is whether the difference $D = 2\mathcal{L}_1 - 2\mathcal{L}_0$ is large enough to justify accepting the more complicated model. To answer this question we use the result that under fairly general conditions, D has a distribution which is approximately equal to a χ^2 random variable with degrees of freedom equal to the number of extra parameters in the more complicated model. If the probability of observing such a large value of D is less than some predetermined value (often 0.05), then the more complicated model is chosen.

As discussed in Fournier et al. (1990), a robust likelihood-based estimator was developed for the MULTIFAN model so that the standard likelihood ratio test could be applied in the hypothesis tests. While this procedure appeared to perform well on the tuna data in that paper, it is interesting to investigate how well the same hypothesis testing criteria perform for a species with a different life history and with a different parameterization of the proportions at age reflecting a different sampling design. If the significance tests appear to perform well in these two very different situations, it indicates that the hypothesis testing procedure may be expected to perform well in many situations.

As in Fournier et al. (1990), we have employed the 0.10 significance level for choosing the number of significant age classes in the model and the 0.05 significance level for all other parameters.

While in theory the likelihood ratio test provides a useful method for deciding whether to include a parameter or group of parameters into the model hypothesis, in practice it can be rather confusing to determine which fits of the model to the data should be retained as candidates for "best" fit. To carry out the hypothesis tests, it is useful to characterize the process of elimination by two rules:

(1) No fit to the data is a candidate for best fit if adding one or more parameters to the model produces a model with a significantly better fit.

(2) No fit to the data is a candidate for best fit if removing one or more parameters from the model produces a model which does not significantly degrade the fit.

It should be emphasized that there is no guarantee that the application of these rules will produce a unique candidate for best fit to the data. For the example considered in this paper, the criteria produced two candidates for best fit. The reason for this ambiguity is discussed below.

Results of the Analysis and Discussion

The process of eliminating fits from consideration as candidates for best fit is tedious at best. A computer program which carries out this task automatically has been developed for the MULTIFAN model. To help the reader understand the mechanics of the process, we shall describe the elimination procedure as though it were carried out by hand.

TABLE 1. Twice the log-likelihood function $\mathcal{L}$ and number of parameters (in parentheses) for four model hypotheses. LISD = length-independent standard deviations; LDSD = length-dependent standard deviations; FRn = full recruitment at age n.

Number of age classes	LISD FR1	LISD FR2	LISD FR2	LDSD FR3
3	1454.86	1495.14	1507.19	1507.19
	(12)	(13)	(14)	(15)
4	1490.42	1528.92	1532.80	1533.05
	(13)	(14)	(15)	(16)
5	1499.04	1533.90	1535.32	1535.35
	(14)	(15)	(16)	(17)
6	1500.40	1533.14	1533.89	1533.88
	(15)	(16)	(17)	(18)
7	1500.18	1532.03	1532.49	1532.72
	(16)	(17)	(18)	(19)

MULTIFAN was used to resolve the Gulf of Maine northern shrimp trawl survey length frequencies to age classes under model alternatives 1 and 2 and the results compared with the previous interpretations of the data by simple visual inspection of length modes (Terceiro and Idoine 1989; NSTC 1989). The results of the analysis for models 1 and 2 were generally similar, except that as one might expect the best fits for model 1 tended to have more age classes in them. Since we feel that the model 2 formulation is more practical for fisheries management applications, we have only presented the model 2 results here.

The values of twice the log-likelihood function ($\mathcal{L}$) for four combinations of model parameters for the model 2 formulation are given in Table 1. The "best" fit to the data within each of the model formulations is underlined. To see how the best fit for each model formulation is determined, consider column 1 in Table 1. Moving from the four age class fit to the five age class fit increases the value of twice the log-likelihood function ($\mathcal{L}$) from 1490.42 to 1499.04, a difference of 8.62, and adds one parameter to the model. Since the 0.90 significance level for one additional parameter is 2.70, this is significant and the four age class model is rejected. Since adding additional age classes does not produce a significant improvement to the fit, the five age class solution is not rejected. Thus the use of rule 1 eliminates the four age class fit. Now consider the six age class fit. Since the six age class fit does not fit significantly better than the five age class fit, the six age class fit is rejected. Similarly, rule 2 can be used to eliminate the seven age class fit.

Similar arguments can be used to pick the "best" fits in the other columns. This is generally the fastest and easiest way to do the hypothesis tests — first eliminate as many fits as possible from each column. Now consider the best fit in the third row of column 1 (five age classes, full recruitment at age 1, length-independent SD: $2\mathcal{L} = 1499.04$). The fit in the third row of column 2 can be regarded as being derived from the fit in the third row of column 1 by including age selectivity on the first age class. This increase the value of $2\mathcal{L}$ from 1499.04 to 1533.90, an increase of 34.86. The inclusion of age selectivity on the first age class involves the addition of one more parameter in the model. Since the 0.95 significance level for one additional parameter is 3.84, this is significant and the model in column 1 is rejected.

Now consider the model in row 2 of column 4. This model does not produce a significant improvement in fit over the model in row 2 of column 3, so it can be rejected by rule 2.

TABLE 2. Parameter estimates for the four and five age class models.

	Age 1	Age 2	Age 3	Age 4+	Age 5+
Four or more age classes					
Mean length (mm)	15.65	20.63	23.99	26.25	
SD	1.15	1.32	1.44	1.53	
Selectivity	0.41	1.00	1.00	1.00	
Five or more age classes					
Mean length (mm)	15.67	20.65	23.80	25.79	26.99
SD	1.24	1.24	1.24	1.24	1.24
Selectivity	0.42	1.00	1.00	1.00	1.00
	4+ age classes			5+ age classes	
L_∞	31.0			29.2	
K	0.39			0.45	
Z	0.72			0.72	

TABLE 3. Estimated proportion at age for the four and five age class models.

	Sample					
	1	2	3	4	5	6
Four age classes						
Age 1	0.07	0.23	0.22	0.21	0.64	0.15
Age 2	0.74	0.12	0.33	0.32	0.14	0.68
Age 3	0.10	0.52	0.07	0.20	0.09	0.06
Age 4+	0.09	0.13	0.38	0.27	0.13	0.10
Five age classes						
Age 1	0.10	0.23	0.22	0.21	0.64	0.16
Age 2	0.67	0.15	0.33	0.32	0.14	0.68
Age 3	0.12	0.46	0.09	0.20	0.09	0.06
Age 4	0.09	0.27	0.27	0.05	0.06	0.04
Age 5+	0.02	0.09	0.09	0.22	0.08	0.06

This leaves two fits, the four age class fit for length-dependent standard deviations and selectivity on the first age class in row 2 of column 3 ($2\mathcal{L} = 1532.80$), and the five age class fit with constant standard deviations and selectivity on the first age class in row 3 of column 2 ($2\mathcal{L} = 1533.90$). The parameter estimates for the two models are given in Tables 2 and 3.

It is easy to see that these two fits offer consistent alternative interpretations of the data. For the four age class fit the model chooses increasing standard deviations with age. This allows a larger standard deviation for the last age class which is interpreted as containing shrimp of four or more age classes. For the five age class fit the model chooses length-independent standard deviations and the fifth age class, consisting of five or more age classes. One can interpret this difference as evidence that the animals are still growing slightly between age classes 4 and 5. The parameter estimates as they pertain to the first three age classes are extremely similar for the two models.

If the estimated proportions at age for age classes 4 and 5+ are added together for the five age class model, the results are almost identical to those obtained for age class 4+ for the four age class model. The predicted fit to the length frequency histograms for the four age class model with length-dependent standard deviations is shown in Fig. 1. The observed length frequency data are represented by the shaded histograms. The broken vertical lines represent the estimated mean lengths at age in each sample. The inner smooth curves are the estimated

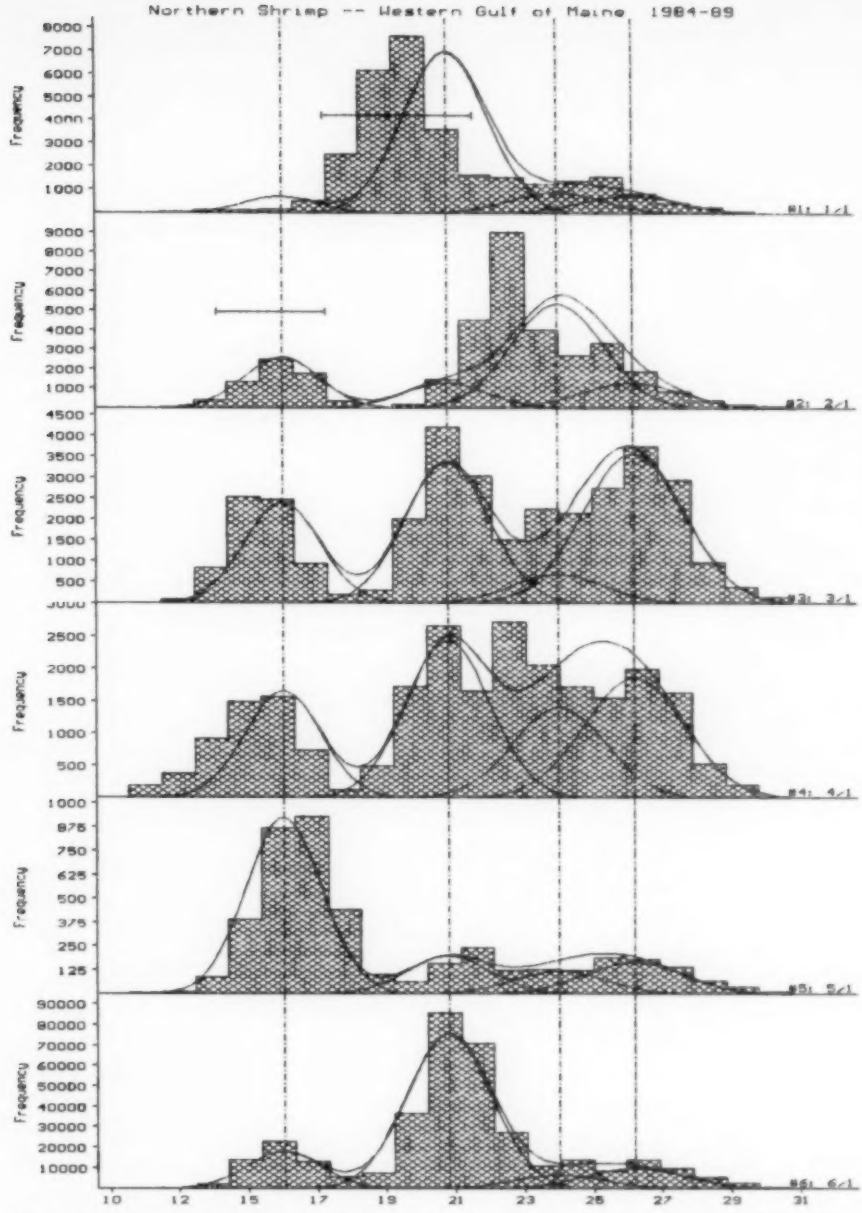

FIG. 1. Length (mm) frequency distribution of northern shrimp in the western Gulf of Maine, 1984–89.

numbers at age and the outer smooth curve is the estimated frequency distribution. The two horizontal lines, bounded by small vertical lines, represent constraints placed on the mean length estimates associated with the corresponding mode.

Two aspects of the fit are apparent from Fig. 1. First, the model is unable to reproduce the observed lengths at age in some cases. For example, the predicted mean length of the shrimp in the second age class in sample 1 is too large. As noted earlier, this 1982 cohort is thought to have grown more slowly than average (Terceiro and Idoine 1989); thus, this particular mode does not match up well with its predicted position using the best fitting model parameters. Second, notwithstanding irregularity in growth between cohorts, MULTIFAN is able to accurately reproduce the proportions at age (obtained with a more detailed knowledge of the species' biology) previously accepted as "ground truth" for these data (Terceiro and Idoine NSTC 1989; Table 4). The main difference between our estimates and those previously derived arise from our more consistent estimate over the time series, using MULTIFAN, of the relative strength of the weak 1983 year class (age class 1 in 1984, age class 2 in 1985, etc.).

A further comparison can be made by the estimation of mortality rates from different age frequencies. For direct compar-

TABLE 4. Estimated numbers in each age class for the four and five age class models and from Terceiro and Idoine (1989) and NSTC (1989).

	Sample year					
	1984	1985	1986	1987	1988	1989
Four age classes						
Age 1	211	807	743	514	2745	545
Age 2	2230	424	1100	792	623	2415
Age 3	290	1832	236	480	393	224
Age 4+	266	464	1281	662	567	346
Five age classes						
Age 1	287	825	746	526	2757	562
Age 2	2023	545	1104	780	622	2396
Age 3	365	1606	305	482	385	226
Age 4	265	290	898	133	238	140
Age 5+	65	262	308	527	326	205
Terceiro and Idoine 1989; NSTC 1989						
Age 1	49	646	710	539	2828	605
Age 2	2051	337	959	575	614	2260
Age 3	442	1596	491	663	187	353
Age 4+	463	952	1200	671	699	474

TABLE 5. Instantaneous total mortality (Z) and corresponding annual mortality rates (A) for ages 2 and older northern shrimp, calculated from numbers at age estimated by MULTIFAN four and five age class models and by Terceiro and Idoine (1989) and NSTC (1989) using the method of visual inspection of length modes.

		Sample year				
		1985	1986	1987	1988	1989
MULTIFAN						
Four age classes	Z	0.19	0.58	0.83	0.70	1.02
	A(%)	17	44	56	50	64
Five age classes	Z	0.23	0.58	0.83	0.71	1.01
	A(%)	23	44	56	51	64
Terceiro and Idoine 1989; NSTC 1989						
Four age classes	Z	0.15	0.53	0.69	0.77	0.60
	A(%)	14	41	50	54	45

ison with previous estimates (Terceiro and Idoine 1989), we calculated "pooled" estimates of the instantaneous total mortality rate (Z) for ages fully recruited to the survey gear (ages 2 and older) for the four and five age class models where

$$Z = \ln\left(\sum_{j\geq 2} N_{ij} / \sum_{j\geq 3} N_{i+1,j}\right).$$

It should be emphasized that we do not recommend estimating Z in this fashion. The estimates of Z obtained within MULTIFAN utilize all the information in the data and are not dependent on stationarity assumptions such as constant recruitment.

In the calculation and comparison of mortality rates, minor differences in the estimated age frequencies are magnified. These effects can be seen in the different rates determined for 1989 from the alternative interpretations of the data, with MULTIFAN catch per tow at age estimates providing a significantly higher Z in 1989 (Table 5).

Differences in the interpretation of length frequency data can have important implications for the assessment of the stock when subsequently derived mortality rates are evaluated in the context of traditional fisheries biological reference points such as $F_{0.1}$ and F_{max}. As noted earlier, the relative abundance data from the NEFC R/V *Gloria Michelle* summer trawl survey are the primary source of stock information used in stock assessment of Gulf of Maine northern shrimp. The less sophisticated methods currently used to analyse these length frequency data require varying degrees of subjective interpretation by fishery scientists to produce reasonable results (Terceiro and Idoine 1989; NSTC 1989). Given the comparison of results using current methods with those from the application of MULTIFAN, it is clear that the key advantage to the use of MULTIFAN with trawl survey data for northern shrimp lies in the ability of the MULTIFAN user to produce equally "accurate," but more objective, estimates of age frequency and mortality rates. Increased objectiveness in the estimation of vital parameters for Gulf of Maine northern shrimp represents an advancement of assessment methodology which may instill greater confidence in the measures relied upon to determine the status of the resource.

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Assessing the Potential Extent of Damage to Inland Lakes in Eastern Canada due to Acidic Deposition. IV. Uncertainty Analysis of a Regional Model[1]

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Jones, M. L., C. K. Minns, D. R. Marmorek, and K. J. Heltcher. 1991. Assessing the potential extent of damage to inland lakes in eastern Canada due to acidic deposition. IV. Uncertainty analysis of a regional model. Can. J. Fish. Aquat. Sci. 48: 599–606.

In this paper, we consider the significance of uncertainty in inputs to the regional surface water acidification model of Marmorek et al. (1990. Can. J. Fish. Aquat. Sci. 47: 55–66). Monte Carlo methods are used to propagate input uncertainty through to measures of uncertainty in the model's overall predictions. We consider four key inputs which represent primary areas of input uncertainty: acidic sulphate deposition (D_a), original lake sulphate concentrations ($[SO_4]_0$), a watershed neutralization parameter (F_W), and an in-lake neutralization parameter (S_S). The analysis is repeated for secondary watersheds from north-central Ontario, the Quebec Laurentians, and insular Newfoundland. Uncertainty in D_a and $[SO_4]_0$ consistently overwhelms the effect of uncertainty in F_W and S_S on overall model uncertainty. The relative importance of D_a decreases as one moves east from the high-deposition regions of central Ontario. We discuss the implications of our results for priority setting for future acidification research and monitoring.

Nous examinons dans cet article la signification de l'incertitude dans les entrées du modèle d'acidification des eaux de surface par région de Marmorek *et al.* (1990. J. can. sci. halieut. aquat. 47 : 55–66). Des méthodes de Monte Carlo sont appliquées à la propagation de l'incertitude dans les entrées jusqu'aux mesures de l'incertitude dans les prévisions d'ensemble du modèle. Nous examinons quatre entrées essentielles qui constituent des domaines primaires d'incertitude; ce sont : les dépôts sulfatés acides (D_a), la concentration originale de sulfate dans les lacs ($[SO_4]_0$), un paramètre de neutralisation caractéristique du bassin hydrographique considéré (F_W) et un paramètre de neutralisation du lac considéré (S_S). L'analyse est reprise dans le cas de bassins hydrographiques secondaires de la région du centre-nord de l'Ontario, de la partie québécoise des Laurentides et de l'Île de Terre-Neuve. L'effet de l'incertitude associée à D_a et à $[SO_4]_0$ domine constamment l'effet de l'incertitude associée à F_W et à S_S sur l'incertitude d'ensemble du modèle. L'importance relative de D_a diminue à mesure que l'on se dirige vers l'est à partir des régions de dépôt intense du centre de l'Ontario. Nous examinons la signification de nos résultats pour l'établissement des priorités en matière de recherche et de surveillance continuelle futures pour ce qui est de l'acidification.

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Concern during the past decade over the problem of long-range transport of atmospheric pollutants (LRTAP) has led to the development of regional models of acidic emission effects on poorly buffered surface waters (e.g. Small and Sutton 1986; Alcamo et al. 1987; Hornberger et al. 1989). These models are designed to simulate changes in surface water chemistry of the population of lakes in a region due to changes in acidic emissions from distant sources. In this way they allow decision makers to examine the potential ecological benefits to be derived from various acidic emission reduction strategies, and thus evaluate acid deposition abatement policies.

Recently, a simple regional model of this type has been developed for sensitive surface waters in eastern Canada (Marmorek et al. 1990; Jones et al. 1990). The model combines simple long-range transport and surface water acidification

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models with a regionalization framework (i.e. a basis for extrapolating from individual lakes to the population of lakes in a region). Using this model, Jones et al. (1990) examined the potential benefits to lakes of eastern Canada of two proposed emission reduction strategies. More recently, Minns et al. (1990) extended the model to include the effects of the predicted changes in water chemistry on aquatic biota, including fish populations.

Although these models provide powerful tools for policy analysis, their credibility can be compromised by the uncertainty associated with estimates of the parameters and inputs they require. Obtaining regionally representative data on historical lake conditions, aggregate measures of lake sensitivity, and accurate estimates of acidic deposition can be extremely difficult and prohibitively expensive. Therefore, it is important to have some idea of the sensitivity of the models being used to the uncertainty in their inputs and parameters. As well as providing an assessment of the credibility of the model(s) in question, an uncertainty analysis can help set priorities for future research and data collection.

There are a variety of techniques available for examining the sensitivity of a model to uncertainty in its parameters and inputs. We have elected to use Monte Carlo methods (O'Neill et al. 1980; Hornberger and Spear 1981), since they allow explicit evaluation of the *relative* uncertainty in model inputs and parameters. The approach involves running a large number of simulations of the same model while allowing selected inputs and parameters to vary from one simulation to the next according to some prespecified uncertainty distribution. The variance in model outputs among simulations is a measure of the sensitivity of the model to uncertainty in the inputs and parameters of interest.

Monte Carlo techniques have been applied to other regional acidification models. Hornberger et al. (1989) used the approach to, in effect, calibrate a regional form of MAGIC (Model of Acidification of Groundwater in Catchments) to surveyed lake chemistry data from southern Norway. By running numerous simulations of MAGIC while allowing model inputs to vary according to prespecified uncertainty distributions, they were able to select input combinations that produced model predictions consistent, on a regional scale, with observed lake chemistry. In contrast, our purpose here is to use the approach to determine the relative sensitivity of our model to uncertainty in various model inputs, and thereby provide an objective rationale for setting priorities for reducing uncertainty.

Although techniques now exist for the application of Monte Carlo methods to complex models with many uncertain inputs (e.g. Latin hypercube designs), interpretation of the results of such analyses can be very challenging. Fortunately, the regional acidification model of interest here is, of necessity, relatively simple. To be useful, the model had to be applicable on a large scale; this meant that the parameter and input requirements were kept to minimum during the model's development. A model of this type is therefore ideally suited to a numerically intensive uncertainty analysis. In this paper we present the results of an investigation of the uncertainty in several of the inputs and parameters for the model described by Marmorek et al. (1990).

Methods

Regional Model

The regional model consists of a single lake, "site" model, a transfer matrix to estimate region-specific acidic sulphate deposition given specified source emission levels, and a regionalization framework. The site model is derived in Marmorek et al. (1990), while the use of the transfer matrix and the regionalization procedure is described in Jones et al. (1990). Readers are referred to these publications for details of the regional model's development.

Briefly, the site model predicts the expected eventual alkalinity ($[Alk]_\infty$) for an individual lake, based on estimates of the lake's original alkalinity ($[Alk]_0$) and the change in alkalinity ($\Delta[Alk]$) due to acidic sulphate deposition. Changes in alkalinity are governed by acidic sulphate deposition rates (D_a), runoff rates (R), and aggregate parameters representing both watershed (F_W) and in-lake (F_L) neutralization processes. Original alkalinity is estimated from current lake chemistry, assumptions regarding original lake sulphate concentrations, and the principle of charge balance. Finally, eventual pH is calculated from alkalinity using an empirical titration curve that closely fits observed pH–alkalinity data from extensive lake surveys.

The transfer matrix is derived from an atmospheric long-range transport model (Olson et al. 1983). The matrix describes the (presumed) linear relationship between emissions from 40 source regions throughout North America and deposition at nine receptor sites. In this paper we will not be considering uncertainty in the transfer matrix; uncertainty in atmospheric transport models has been the subject of other investigations (e.g. Ellis 1988).

Regional application of the site model requires specification of the distributions of the model inputs and parameters among the population of lakes in a region of interest. Jones et al. (1990) chose secondary watersheds as the appropriate spatial unit for regionalization. Water chemistry and hydrological and topographical survey data were used to describe the distributions of those parameters assumed to vary among lakes on this spatial scale. Regionalization involves using these distributions to divide all the lakes in a secondary watershed into discrete classes, running the site model on each class of lake, and scaling the results back up to the watershed level according to the fraction of lakes in the watershed represented by each class. The result is a predicted distribution of eventual lake chemistry (alkalinity or pH) for each secondary watershed.

Selection of Model Inputs and Parameters for Uncertainty Analysis

The regional model's predictions contain four sources of uncertainty, or potential error: (1) regionalization error (i.e. differences between the characteristics of the modelled population of lakes and those of the actual population); (2) measurement errors in the model inputs (e.g. watershed and lake areas, lake chemistry, runoff); (3) errors in the assumed values of model parameters which determine how lake chemistry responds to deposition (F_W, F_L); and (4) errors in model structure. Regionalization error reflects both sample bias (application of the model to a subsample of lakes which were not chosen from a probability sample, and therefore may not be representative of the true population of lakes in the secondary watershed) and sample precision (differences between the modelled and actual population of lakes due to modelling only a low number or proportion of the lakes in some secondary watersheds). Errors in model structure can only be determined through tests of model predictions and assumptions, some of which are described in Marmorek et al. (1990). This paper,

TABLE 1. Distribution assumptions for the four model inputs and parameters allowed to vary in the Monte Carlo analysis.

Parameter	Watershed	Lower bound	Upper bound	Modal value	Distribution type
Deposition (D_a)	2C	10.21	58.70	32.62	Triangular
	2S	3.28	46.36	23.18	Triangular
	2Y	2.07	29.28	14.64	Triangular
$[SO_4]_0^*$	All	10	100	—	Uniform
b	All	50	1000	—	Uniform
S_s	All	0.36	0.54	—	Uniform

*Actually D_a/R.

while recognizing regionalization and model structure uncertainties, concentrates on describing the effects of uncertainties in model inputs and parameters.

Most of the model's inputs (watershed and lake areas, current lake chemistry, runoff) have been measured with reasonable precision. In contrast, there is considerable uncertainty in our estimates of D_a at the secondary watershed level, whether predicted from the transfer matrix models or derived by interpolation from existing deposition monitoring stations. Equally uncertain are estimates of nonacidic sulphate deposition (D_n), which are used to calculate original sulphate ($[SO_4]_0$). As well, specifying some model parameters has required "educated assumptions" based on the results of more localized, intensive studies of the processes involved in surface water acidification.

Marmorek et al. (1990) briefly considered the sensitivity of the model to two parameters: ($[SO_4]_0$) and the parameter b, which is used to estimate the value of F_W (equation 4 of Marmorek et al. 1990). Here we extend the analysis of uncertainty to include two other model components: D_a and S_S, the mass transfer coefficient that determines F_L, the fraction of sulphur deposition converted to alkalinity by in-lake sulphur reduction. These four variables ($[SO_4]_0$, b, D_a, and S_S) are the ones about which we have the greatest uncertainty for the overall target population of lakes.

To examine whether the relative importance of these four model inputs differs among regions of eastern Canada, we have repeated the Monte Carlo analysis for three secondary watersheds: 2C (Algoma–Sudbury area, north-central Ontario), 2S (Quebec Laurentians), and 2Y (insular Newfoundland). These three areas represent wide contrasts in estimated deposition rates and in average present-day lake chemistry.

Specification of Uncertainty in Input Variables

For each of the four model inputs and parameters chosen for the uncertainty analysis, we need to describe our uncertainty regarding their true value in the form of a probability distribution of expected values. These distributions form the inputs for the Monte Carlo analysis, as described below. For one of the four variables (D_a), we expect these probability distributions to differ among the three secondary watersheds of interest. For our purposes here, we have described each distribution in terms of its form (i.e. shape) and its upper and lower bounds (Table 1).

As mentioned earlier, we have chosen not to consider the uncertainty in predictions of deposition rates due to uncertainty in existing atmospheric transport models. Instead we are considering uncertainty in observed deposition rates (1980 data); observed 1980 deposition rates were used in the "baseline" scenarios of Jones et al. (1990). The uncertainty associated with these observations stems primarily from the interpolation required to estimate deposition at a location some distance from the nearest deposition monitoring station. Actual measured wet sulphate deposition and air sulphur concentrations from CAPMoN sites throughout eastern Canada were interpolated to a half-degree latitude–longitude grid using a statistical procedure known as kriging (cf. Finkelstein 1984). These interpolated values were then used to determine the deposition at the centroid of each secondary watershed in sensitive regions of eastern Canada.

Clark et al. (1987) examined the uncertainty associated with the kriging procedure, using the 1980 deposition data. They determined that errors of ±50% could be expected in regions containing several monitoring sites. In more remote regions, where monitoring stations are more sparsely distributed, the error increases to ±100%. On the basis of their analysis, we have assumed a range of error in deposition of ±80% for watershed 2C and ±100% for watersheds 2S and 2Y. We have used a triangular distribution to describe this uncertainty; Tiwari and Hobbie (1976) suggested that when the true distribution of a parameter is unknown, but a most probable value has been estimated, a triangular distribution represents the least-biased assumption.

The two studies in which S_S values have been calculated resulted in three different estimates for this parameter. Baker et al. (1986) measured S_S to be 0.46, while Kelly et al. (1987) estimated a value of 0.36 from sulphate flux calculations and a value of 0.54 from mass balance calculations. We have chosen the two values from the latter study as the bounds of our uncertainty in this variable. Since we have no basis upon which to assume a most probable value for S_S within this range, we have used a uniform probability distribution in this case.

In our earlier sensitivity analysis (Marmorek et al. 1990), we allowed the value of b to vary from 200 to 1000 μeq/L. In the site model, lakes whose original base cation concentrations ($[C_B]_0$) are greater than b are assigned a value of 1 for F_W, implying complete watershed neutralization of acidic sulphate deposition. Recent paleolimnological studies in the Adirondack Mountains of New York State (Sullivan 1990) suggested that lakes with $[C_B]_0$ and $[Alk]_0 > 50$ μeq/L have experienced negligible historical changes in alkalinity. These results have led us to reduce the lower bound on b from 200 to 50 μeq/L.

Following Marmorek et al. (1990), we have chosen a range of values for $[SO_4]_0$ based on observed variations in $[SO_4]_t$ in remote regions where sulphate concentrations are unlikely to have changed due to anthropogenic inputs. In the site model, $[SO_4]_0$ is calculated from

$$(1) \quad [SO_4]_0 = \frac{D_n}{R}(1 - F_L).$$

Marmorek et al. (1990) allowed $[SO_4]_0$ to vary from 10 to 100 μeq/L; here we have assumed instead that D_n/R varies from 10 to 100 μeq/L. This avoids the problem of having to allow $[SO_4]_0$ and S_S to vary independently, which would be inconsistent with the above eqution, since F_L depends on S_S. For both b and D_n/R we have used a uniform distribution due to the absence of a basis for determining a "most probable" value.

Analytical Methods

To carry out the Monte Carlo analysis, we used the probability distributions for each of the variables of interest to randomly select a series of 1000 independent combinations of values. By using this approach, we are assuming that all four

parameters vary independently of one another. We argue that this is the most reasonable assumption to make, for two reasons. First, there is no obvious reason to assume that any of the four inputs is functionally linked to any of the others. Acidic sulphate deposition is anthropogenically derived from industrialized areas, while most nonacidic sulphate (and therefore $[SO_4]_0$) is either nonanthropogenic or derived from rural sources. S_S is a lake characteristic, while b depends on features of the lake's catchment. Second, if the inputs do covary, then our assumption of independence will overestimate our overall uncertainty and is thus the more conservative assumption to make. Given the significance of the regional model's predictions to policy, we have chosen throughout its development and analysis to be conservative, both in our estimation of impacts and in our assessment of uncertainty.

We carried out the Monte Carlo analysis by running the model 1000 times for each watershed, choosing the next set of input values from our random series of 1000 for each successive run. The regional model outputs comprise distributions of eventual alkalinity and pH for the population of lakes in the secondary watershed. To facilitate our analysis of outputs we selected from these distributions two model output indicators as the basis for describing the uncertainty in predictions: (1) the proportion of lakes in the region with predicted eventual alkalinity less than zero and (2) the proportion of lakes in the region with predicted eventual pH less than 5.5. These two measures provide examples (although not the only examples, since losses of some taxa have been shown to occur at pH $<$ 6.0) of ecologically relevant indicators of acidification on the lakes in a watershed. To facilitate comparison of the results among different sets of simulations, we have applied an arcsine square root transformation to normalize the output distributions.

The principal objective of this study was to examine the relative influence on overall model uncertainty of each of the four input variables of interest. To address this question, we repeated the Monte Carlo simulations four additional times, each time holding one of the four input variables constant (at the mean value for its uncertainty distribution). By measuring the amount by which uncertainty in model outputs is reduced when a particular input is assumed to be known (i.e. held constant), one obtains an estimate of the marginal contribution of each parameter to overall model uncertainty.

Results

When all four model inputs are allowed to vary according to the distributions described above, the resulting range in model outputs is quite high (Fig. 1). The coefficients of variation for the two output indicators range from 24 to 48%. This uncertainty is sufficient to suggest that a significant (from a policy standpoint) increase in confidence could be achieved by reducing the uncertainty in at least some of these model inputs. On the other hand, it is at least as important to note that this uncertainty does not span a range that includes both minimal and substantial impacts. For example, 75% of the Monte Carlo simulations for watershed 2S produced results ranging from 35.5 to 56.4% of lakes with predicted eventual alkalinity less than zero. Any prediction within this range would almost certainly be considered indicative of substantial impacts.

As a simple indication of the relative contribution of each of the four model inputs to overall model uncertainty, we have calculated the correlation between each of the model input variables and the (transformed) output indicators. These correlations (Table 2) indicate that variations in D_a and $[SO_4]_0$ explain most of the variation in model outputs for all three watersheds. Variations in parameter b never account for more than 5% of the variability in model outputs, while for S_S the value is consistently less than 1%. There is also an obvious gradient in the relative importance of D_a and $[SO_4]_0$, with the former being most important in watershed 2C, where deposition is greatest (on average). As one moves eastward, $[SO_4]_0$ becomes increasingly important and dominates D_a in watershed 2Y.

The use of a correlation matrix for this purpose is not ideal, since it assumes that any association between input variable and model output uncertainty is linear. A more general approach is to calculate the reduction in the variability in model outputs (here represented by a reduction in the coefficient of variation in transformed model outputs) which results from holding one of the uncertain model inputs constant. If the effect of uncertainty in an input variable is large, then eliminating the uncertainty in this manner should result in a considerable decrease in the variability of model outputs.

Comparisons of the coefficients of variation (CV) among Monte Carlo runs with each of the four model inputs held constant (Fig. 2) confirm the impression gained from examination of the correlation matrix. Holding acidic sulphate deposition or $[SO_4]_0$ constant substantially reduces the CV in all three watersheds; the previously noted east–west gradient of relative importance of these two inputs is evident here as well. Relative to uncertainty in deposition and $[SO_4]_0$, uncertainty in the "lumped process" parameters (b and S_S) appears to have very little influence on model output uncertainty, in all cases examined.

Discussion

Models of the regional scale impacts of widespread environmental stresses, such as acidic deposition, provide extremely valuable tools for assessment. To be properly used for such assessments, however, careful attention must be paid to the uncertainties inherent in such models. At least as important as the "best guess" predictions of the impacts of various changes in acidic deposition is an explicit consideration of the range of possible predicted outcomes that are consistent with existing uncertainties in the models being used. Thus, uncertainty analyses such as those presented above have a key role to play in the overall assessment process.

Our analysis suggests that of the model inputs and parameters considered here, the two associated with atmospheric sources have the greatest influence on model uncertainty. One of these, acidic sulphate deposition, is most important in the westernmost watershed considered (2C), where deposition rates are, on average, highest. This result occurred despite our assumption that the variance in D_a was somewhat less in watershed 2C than farther east. This illustrates the difference between the uncertainty in a model input and the model's sensitivity to that input. As D_a becomes larger, its influence on $[Alk]_\infty$ increases relative to that of other variables such as $[SO_4]_0$; this is equivalent to saying the model's *relative* sensitivity to D_a increases as D_a itself increases. Thus the effect of increasing the average value of D_a overwhelms the effect of reducing its variance.

Our method of defining uncertainty in D_a may actually yield an underestimate, for two important reasons. First, as noted earlier, we are only considering uncertainty in observed deposition rates, not those predicted from long-range transport models. This latter uncertainty may well be comparable with

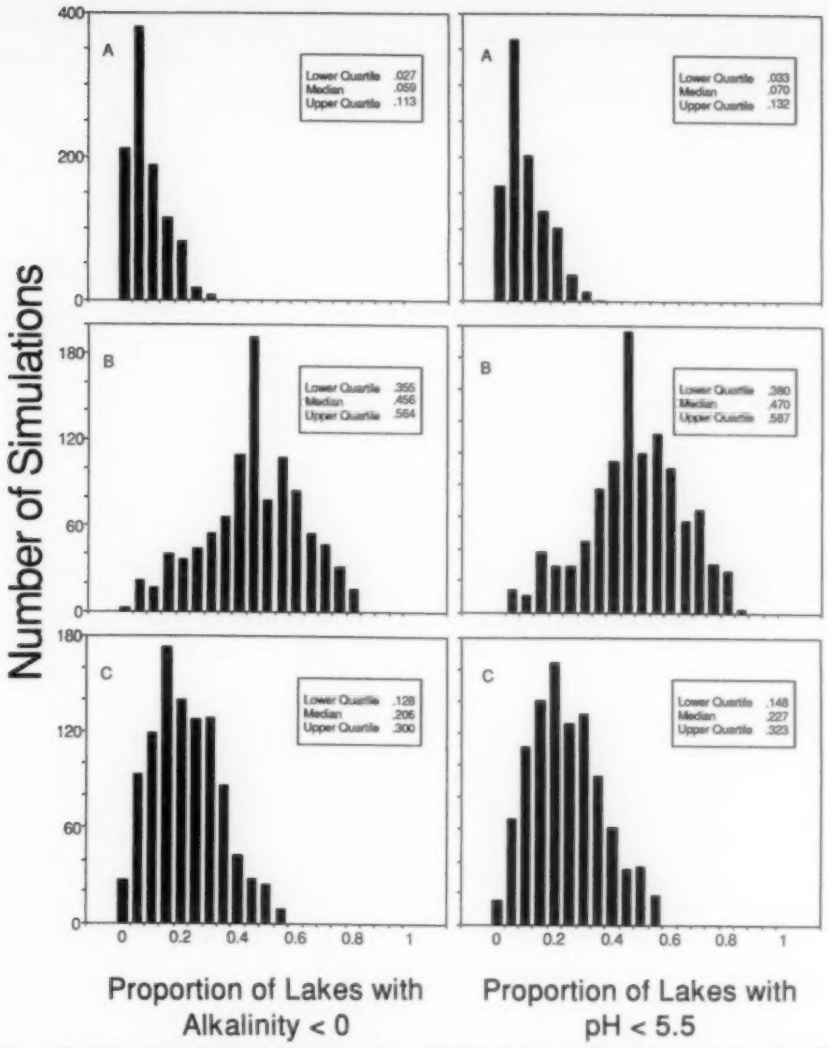

FIG. 1. Frequency distributions of the proportions of lakes with eventual alkalinity < 0 or pH < 5.5 as predicted from 1000 Monte Carlo simulations when all four model inputs and parameters were allowed to vary. (A) Watershed 2C; (B) Watershed 2S; (C) Watershed 2Y. Also shown for each case are the median proportions and the lower and upper quartiles.

TABLE 2. Multiple r^2 values for the correlation between variable model inputs and model output indicators (Alk and pH) for each of the three secondary watersheds (2C, 2S, and 2Y) included in the Monte Carlo analysis.

	2C		2S		2Y	
	Alk < 0	pH < 5.5	Alk < 0	pH < 5.5	Alk < 0	pH < 5.5
Model inputs						
D_a	0.663	0.655	0.468	0.460	0.314	0.307
$[SO_4]_0$	0.276	0.271	0.470	0.473	0.676	0.681
b	0.040	0.047	0.026	0.030	0.010	0.013
S_s	0.007	0.007	0.002	0.002	0.002	0.003

that associated with interpolating observed deposition values. This implies that our uncertainty analysis is most appropriately considered relevant to cases in which observed monitoring network deposition data are available. There will be additional uncertainty associated with regional model predictions of the response to an emissions control strategy (cf. Jones et al. 1990). Second, we have ignored the uncertainty in converting air concentrations to dry sulphur deposition rates. Little is known regarding the uncertainty in the deposition velocity estimates required to make this conversion; it is likely to be quite high given the substantial methodological problems aassociated with measuring dry deposition. If dry deposition uncertainty were to be added, it would probably exaggerate the west–east gradient in the relative importance of D_a, since dry deposition tends to become an increasingly minor fraction of total deposition as one moves further from major emissions sources.

Uncertainty in our estimates of $[SO_4]_0$ also has a large relative influence on model predictions, especially in the more remote watersheds. This result is consistent with the results presented in Marmorek et al. (1990) where the model's sensitivity to $[SO_4]_0$ and b was examined. The results seen here are

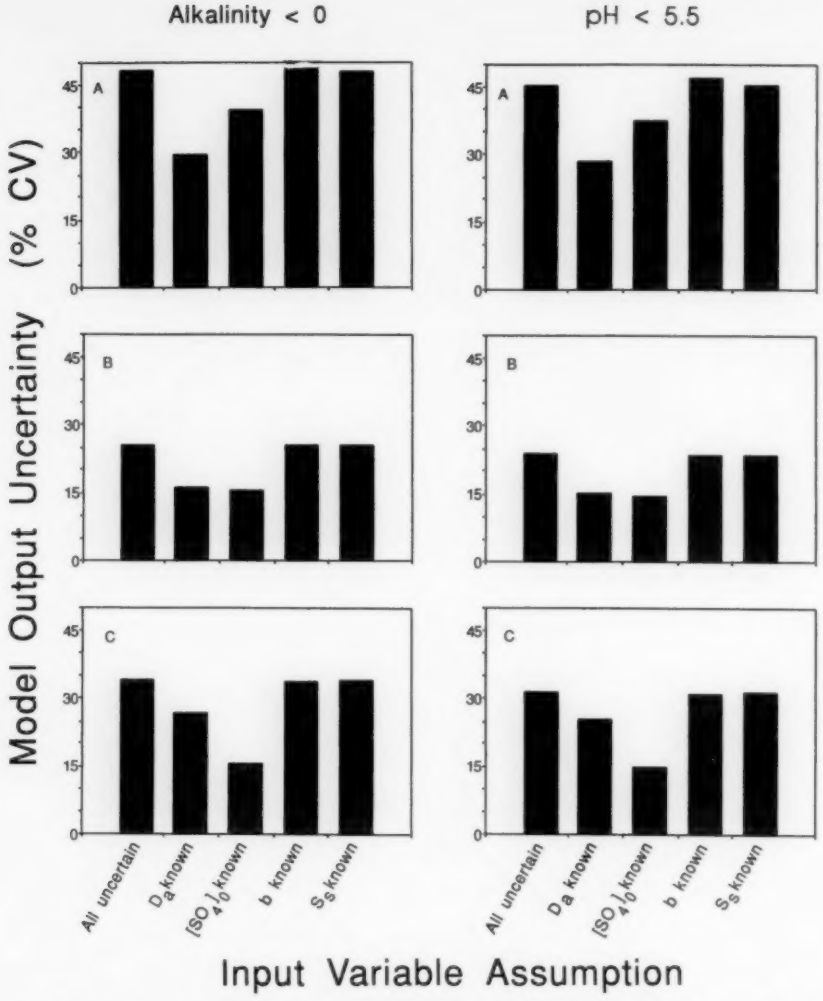

FIG. 2. Overall model uncertainty, expressed as the percent coefficient of variation in arcsine square root transformed proportions of lakes with alkalinity < 0 or pH < 5.5, for the case in which all four model inputs are allowed to vary and for cases in which one input is held constant (i.e. assumed known). The reduction in output uncertainty resulting from holding a particular input constant is a measure of the significance of uncertainty in that input. (A) Watershed 2C; (B) Watershed 2S; (C) Watershed 2Y.

a consequence of two things: (1) the model is sensitive to variations in original sulphate and (2) we are highly uncertain about the value of this input variable. As shown in Marmorek et al. (1990), the sensitivity of eventual alkalinity to original sulphate is given by

$$(2)\quad \frac{\partial[Alk]_\infty}{\partial[SO_4]_0} = -1 + \left[1 + \frac{D_a}{R}\left(\frac{r}{r+1}\right)\left(\frac{1}{b}\right)\right]\left(\frac{r}{r+1}\right)\left(\frac{F_w}{(1-F_L)}\right)$$

where r is the ratio of watershed area to lake area. For low values of F_W, relative to $(1 - F_L)$, changes in eventual alkalinity are most sensitive (nearly inversely proportional) to changes in original sulphate. Thus, lakes within watersheds having limited acid neutralization potential (F_W), as indicated by cation export ($[C_B]$), are particularly sensitive to changes in the assumed or estimated value of $[SO_4]_0$. Further, Equation 2 indicates that the sensitivity of eventual alkalinity to $[SO_4]_0$ increases as D_a becomes smaller, or as R (runoff) becomes larger, provided

$$\left(\frac{D_a}{R}\right)\left(\frac{1}{b}\right)$$

is much less than 1, as will be the case on average ($\bar{D}_a$ = 15–33, $\bar{R}$ = 0 .5–1, $\bar{b}$ = 475).

These factors probably explain the observed increase in the relative importance of uncertainty in $[SO_4]_0$ as one moves eastward. Because we assumed that our uncertainty with respect to $[SO_4]_0$ does not vary among watersheds (Table 1), this pattern is presumably explained by variations in the model's sensitivity. Deposition rates decline on a west–east gradient, as do

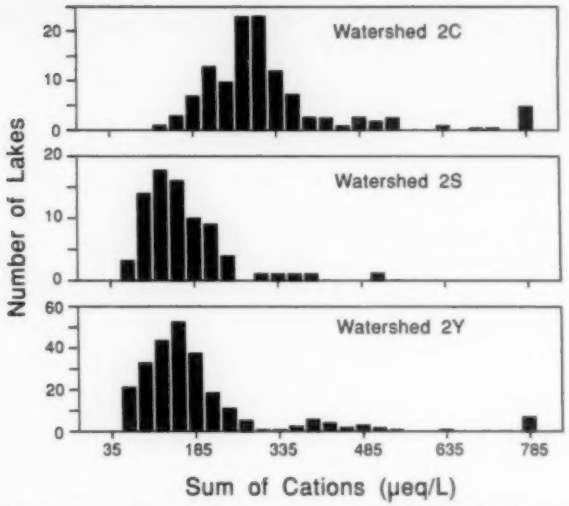

FIG. 3. Observed (from lake survey data) frequency distributions of the sum of base cations (Ca, Mg, Na, and K) for watersheds 2C, 2S, and 2Y.

average lake cation concentrations (Fig. 3), while runoff tends to increase.

The uncertainty range we have assumed for $[SO_4]_0$ for watersheds 2S and 2Y may be greater than is realistic for these areas. The range of 10–100 was derived from the observed range of lake sulphate levels in areas of Canada receiving very little acidic sulphate deposition. Labrador lakes cluster at the low end of this range ($[SO_4]_0$ range of 10–40 μeq/L), while lakes in northwestern Ontario are near the upper end (Kelso et al. 1986). If one can infer from these limited observations on east–west gradient of increasing original sulphate values, then a narrower, and geographically variable, uncertainty distribution for original sulphate might be more appropriate. For the purposes of this analysis, however, we chose to err on the side of overestimating our uncertainty.

Our results suggest that significant improvements in predictive power could be obtained by reducing our uncertainty with respect to D_n and $[SO_4]_0$. Improved accuracy and precision of regional estimates of sulphur deposition requires an increase in the density of the deposition monitoring network, or some independent assessment of the interstation patterns of deposition. Unfortunately, it is impossible to obtain direct estimates of $[SO_4]_0$ for the lakes of interest. It should be possible, however, to increase confidence in the indirect estimates that have been used (Equation 1). Following Brydges and Summers (1989), Jones et al. (1990) used base cation deposition as an indicator of D_n. Better estimates of cation deposition (i.e. data from more than one year) and a more rigorous assessment of whether cation deposition is in fact a reasonable measure of nonacidic sulphate deposition would be extremely valuable. In addition, this method assumes that watershed sources of sulphate are insignificant. To test this assumption, we need more data on the magnitude of watershed sources. Such data can be obtained from sites (such as calibrated watersheds) where sulphate mass balance calculations have been made that include accurate estimates of total sulphur deposition.

It is perhaps surprising to see the relative unimportance of uncertainty in the two model input parameters that represent the watershed and lake neutralization processes (i.e. b and S_s). For individual systems the changes in lake chemistry that would result from changes in acidic sulphate inputs will be sensitive to assumptions about the value of these parameters. On a regional scale, however, it would appear from this analysis that uncertainty in the parameters that determine the inputs of acidity (deposition) and the overall sensitivity of lakes (through the effect of $[SO_4]_0$ on original alkalinity) overwhelm the effects of uncertainty in the two process parameters.

Finally, it is important to reemphasize that the uncertainty analysis presented here is not comprehensive. While the analysis explicitly considers uncertainty in several model inputs, it completely ignores other factors that contribute to our overall uncertainty. For example the scaling of the regional model results to the target population of lakes depends on the untested assumption that the sample of lakes used by the model is representative of this target population and sufficiently large to describe regional distributions of water chemistry precisely. In addition, the analysis assumes that the model is structurally correct and, thus, that all our uncertainty lies with the data (i.e. our estimates of model inputs and parameter values) rather than with the model itself. The assumption of a linear relationship between watershed cation export and F_w is an example of a model component that has a very limited theoretical or empirical foundation.

Further, we have not considered uncertainty in the predicted biological impacts of regional acidification, as discussed in the third paper in this series (Minns et al. 1990). The biological model uses collections of species' absence–presence pH thresholds to construct a percentage curve of potential species richness versus pH, relative to a reference value of 100% at pH 7.0. Variation associated with individual thresholds could be used to estimate the confidence intervals for the potential species richness curve. We expect, however, that application of a rectangular random distribution of as much as ± 0.1–0.2 pH unit about each species threshold would not have greatly altered the predictions of the biological model, given the number of species thresholds involved for each taxonomic group.

On the other hand, there is a second level of uncertainty to be considered when predicting changes in species richness in individual lakes. The biological model used by Minns et al. (1990) depends on the assembly of pH thresholds for large pools of species, pools larger than would occur on individual lakes. Minns (1989) showed that in Ontario watersheds there are on average 5–10 fish species per lake, while there are 30–50 species in tertiary watershed pools. One could argue that when lake acidification occurs, species with high pH thresholds are replaced by more tolerant species in the pool. Many studies, however, have shown for fish and other taxa that species richness is lower in lower pH lakes (e.g. Minns 1989). Extending the potential species richness model to predict species richness and composition in individual lakes is a complex problem, particularly because species richness is also related to other factors such as lake size and depth.

While estimates of the impacts of acidic deposition and associated abatement policies are needed now, as is a measure of the uncertainty in these estimates, in the longer term the assessment process will benefit from an evaluation of sources of uncertainty other than those considered in this study. As future deposition levels change, due to changes in the magnitude and distribution of emissions, well-designed long-term monitoring of deposition, water chemistry, and aquatic biota is essential. It is primarily through such monitoring that we can learn to

what degree real lakes behave like modelled ones and identify the regional significance of errors in model structure.

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Prey Selectivity by Age 0 White Perch (*Morone americana*) and Yellow Perch (*Perca flavescens*) in Laboratory Experiments

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Parrish, D. L., and F. J. Margraf. 1991. Prey selectivity by age 0 white perch (*Morone americana*) and yellow perch (*Perca flavescens*) in laboratory experiments. Can. J. Fish. Aquat. Sci. 48: 607–610.

We conducted prey selectivity experiments by age 0 white perch (*Morone americana*) and yellow perch (*Perca flavescens*) in the laboratory. Lake Erie zooplankters were introduced into tanks where both fishes were in single and combined species assemblages. We identified and counted the introduced plankton samples and the contents of fish stomachs after the feeding period. Our results showed no differences in prey consumed within a fish species, whether in single or combined assemblages (ANOVA, $p > 0.05$). There were a few differences between white perch and yellow perch consumption of each prey taxa (ANOVA); however, the arrays of organisms eaten were not different (MANOVA, $p > 0.01$). We note that the majority of prey consumed were smaller taxa, which is counter to optimal foraging predictions in relation to prey size, but is consistent with other research on young planktivore prey selectivities.

Nous avons procédé à des expériences de sélection des proies par le baret (*Morone americana*) et la perchaude (*Perca flavescens*) de moins d'un an au laboratoire. Des zooplanctontes du lac Érié ont été placés dans des bassins où se trouvaient des poissons en assemblages de chaque espèce ou des deux espèces réunies. Nous avons pratiqué l'identification des espèces et des dénombrements sur des échantillons de plancton introduit ainsi que sur les contenus stomacaux après la période d'alimentation du poisson. Qu'il se soit agi des assemblages d'une seule espèce ou de ceux des deux espèces, nos résultats n'ont montré aucune différence intraspécifique quant aux proies consommées (ANOVA, $p > 0{,}05$). Quant à la consommation de chaque taxon pris comme proie, il existait quelques différences entre le baret et la perchaude (ANOVA); toutefois, les ensembles d'organismes ingérés ne différaient pas (MANOVA, $p > 0{,}01$). Nous constatons que la majorité des proies consommées appartenaient à des taxons de plus petite taille, ce qui est contraire aux prévisions relatives au broutage optimal en fonction de la taille des proies, mais qui correspond à d'autres travaux de recherche sur la sélection des proies par de jeunes planctivores.

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White perch (*Morone americana*), an East Coast estuarine species, were first collected in Lake Erie in 1953 (Larsen 1954), although their numbers did not increase dramatically until the past decade (Boileau 1985; Schaeffer and Margraf 1986). We know white perch and yellow perch (*Perca flavescens*) interact in Lake Erie at age 1 and older from investigation of their food consumption and diet overlap from field collections (Parrish and Margraf 1990). Other age 0 fishes in Lake Erie, e.g. gizzard shad (*Dorosoma cepedianum*), emerald shiner (*Notropis atherinoides*), and spottail shiner (*N. hudsonius*), also feed almost exclusively on zooplankton. Therefore, our objective in this study was to determine feeding preferences of age 0 white perch and yellow perch to aid in predicting how these species partition food resources in their first year of life.

In the laboratory, we conducted prey selectivity experiments with age 0 white perch and yellow perch in which a Lake Erie plankton sample was introduced into tanks occupied by both species. In conducting these experiments, we asked the following: Does each species consume the same prey taxa in the combined assemblage as when alone? Do white perch and yellow perch eat the same prey taxa, whether in single or combined species associations? What prey taxa are eaten and does prey selection match optimal foraging predictions?

Materials and Methods

We collected age 0 white perch and yellow perch by shoreline seining and bottom trawling (2-min tows) in shallow areas (<6 m deep) of the western basin of Lake Erie, near East Harbor and South Bass Island, during August 1986 and September and October 1987. Fish were transported to the laboratory where the experiments were conducted.

Three trials of a prey selectivity experiment by young white perch and yellow perch were conducted in laboratory aquaria in August 1986. We stocked both species into a three-chambered 200-L stream tank in single species ($N = 10$) or combined ($N = 5$ white perch and 5 yellow perch) assemblages.

White perch and yellow perch were held in the laboratory a minimum of 4 d and were acclimated to the experimental tank

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TABLE 1. Numbers of organisms from plankton samples introduced into each compartment or tank during age 0 feeding selectivity experiments in 1986 and 1987. LEP = *Leptodora*, DAP = *Daphnia*, CYC = cyclopoid copepods, CAL = calanoid copepods, EUB = *Eubosmina*, OST = ostracods, and BYT = *Bythrotrephes*.

Year	Trial	Date	LEP	DAP	CYC	CAL	EUB	OST	BYT
1986	1	August 14	5	240	1344	0	288	0	0
	2	August 17	8	128	1216	0	448	5	0
	3	August 27	2	70	310	0	130	48	0
1987	1	September 10	16	284	471	304	2068	0	0
	2	September 15	1060	1970	60	70	30	0	0
	3	September 16	168	536	8	24	8	0	0
	4	September 27	227	1123	11	2	11	0	16
	5	October 19	8	1272	16	0	16	0	96

TABLE 2. Means of individual preference values (Manly/Chesson index) for white perch (WP) and yellow perch (YP) from selectivity experiments in 1986. LEP = *Leptodora*, DAP = *Daphnia*, CYC = cyclopoid copepods, EUB = *Eubosmina*, and OST = ostracods. Preferences > 0.25 in trial 1 and > 0.20 in trials 2 and 3 are underlined, indicating positive selection for a given prey. S = single species, C = combined species, N = number of fish.

				Mean preference value				
S/C	Species	Trial	*N*	LEP	DAP	CYC	EUB	OST
S	YP	1	10	0.21	0.27	0.45	0.05	—[a]
		2	10	0.22	0.26	0.26	0.06	0.20
		3	10	0.21	0.37	0.29	0.10	0.03
C	YP	1	5	0.19	0.43	0.32	0.05	—[a]
		2	5	0.42	0.27	0.30	0.02	0.00
		3	5	0.00	0.41	0.23	0.28	0.10
C	WP	1	4	0.00	0.59	0.41	0.00	—[a]
		2	4	0.19	0.30	0.28	0.00	0.22
		3	4	0.00	0.53	0.28	0.19	0.00
S	WP	1	9	0.13	0.31	0.47	0.08	—[a]
		2	7	0.14	0.26	0.20	0.05	0.35
		3	10	0.00	0.42	0.35	0.22	0.01

[a]Ostracods were not present in the plankton samples.

for at least 24 h. Fish were starved for at least 18–24 h to allow for gut clearance. A plankton sample was collected at dawn with a 118-μm-mesh net using vertical plankton tows. At approximately 0700 h, three 116-mL aliquots were introduced into the partitioned tank. Another three aliquots were preserved in 10% formalin for determining zooplankton abundance and species composition. Plankton in the preserved aliquots were counted and averaged and represent the available organisms for consumption in the samples.

Seven minutes after the prey were introduced and feeding began, we removed and froze all fish. For stomach analysis, fish were thawed, standard lengths (millimetres) recorded, and contents identified and counted. We compared the proportions of prey consumed by the two species with the proportion available in the environment to calculate the selectivities (Manly/Chesson index; Chesson 1978, 1983).

In September and October 1987, five additional trials were run. However, we made some changes in the procedure that should be noted. Fish were stocked in three separate 750-L aquaria. Prior to collection of the plankton sample, each tank was drained to a level of approximately 100 L so that the plankton would be concentrated. Samples were collected just before dawn, towing horizontally with a 505-μm plankton net. Fish were allowed to eat for 10 min, beginning when the first fish initiated feeding. Because of the larger numbers of plankton in these samples, only one aliquot was preserved. Numbers of plankton introduced were obtained by subsampling in triplicate, counting each subsample, and reporting the average. Subsample proportion to the original sample range from 0.1 to 0.2, depending on plankton density.

Results

Species compositions of the plankton samples differed between 1986 and 1987 and within years (Table 1). Although ostracods are usually not considered a part of the plankton, they were collected in two trials in 1986 and were consumed by the fish. Of the Copepoda, only cyclopoids were present in 1986, but both cyclopoid and calanoid copepods were present in 1987. *Bythotrephes*, a recently introduced European cladoceran, was not present in 1986; in 1987, it was present in two trials. *Diaphanosoma* and some chydorids were present in one trial, but were rare, and so were not considered in the selectivity calculations.

In 1986, Manly/Chesson preference index values were similar in prey types eaten within a species (single versus combined assemblages) and between species (Table 2), except yellow perch marginally selected for *Leptodora* and white perch did not, while white perch selected for ostracods and yellow perch did not. Both species selected *Daphnia* and cyclopoid copepods. These patterns were consistent regardless of single or combined species.

The 1987 results (Table 3), although different from those of 1986, did not indicate that single or combined assemblages were a factor. Yellow perch never selected for *Leptodora*, but white perch did once, when the concentration of *Leptodora* was the highest. Neither species selected *Daphnia*, but both ate copepods and to a lesser degree *Eubosmina*. Yellow perch in combined stockings selected for *Bythrotrephes* in one trial.

Data for the three trials in 1986 were pooled for statistical analyses; however, we were not able to pool the 1987 data because of differing prey availability among trials (Table 4). In both years, neither white perch or yellow perch altered their selection of individual prey (ANOVA, $p > 0.05$) or of the array of organisms (MANOVA, $p > 0.01$) according to single or combined assemblages. We tested for differences in preference values of individual prey items consumed between species in 1986, regardless of single or combined stockings. Only one was different; yellow perch ate more *Leptodora* (Table 4). In 1987, significant differences were noted in consumption of *Leptodora*, where white perch ate more than yellow perch, and

TABLE 3. Means of individual preference values (Manly/Chesson index) for white perch (WP) and yellow perch (YP) from selectivity experiments in 1987. LEP = *Leptodora*, DAP = *Daphnia*, CYC = cyclopoid copepods, CAL = calanoid copepods, EUB = *Eubosmina*, and BYT = *Bythotrephes*. Preferences > 0.20 in trials 1–3 and 5 and > 0.17 in trial 4 are underlined, indicating positive prey selection. S = single species, C = combined species, *N* = number of fish.

				Mean preference values					
S/C	Species	Trial	*N*	LEP	DAP	CYC	CAL	EUB	BYT
S	YP	1	10	0.04	0.04	0.40	0.03	0.26	—[a]
		2	10	0.16	0.03	0.44	0.22	0.15	—[a]
		3	5	0.00	0.00	0.51	0.15	0.34	—[a]
		4	1	0.00	0.00	0.50	0.00	0.50	0.00
		5	10	0.01	0.00	0.85	—[a]	0.12	0.03
C	YP	1	0	—	—	—	—	—	—
		2	5	0.07	0.02	0.45	0.24	0.22	—[a]
		3	4	0.00	0.00	0.49	0.50	0.00	—[a]
		4	4	0.00	0.00	0.62	0.31	0.06	0.00
		5	5	0.00	0.00	0.62	—[a]	0.13	0.25
C	WP	1	0	—	—	—	—	—	—
		2	2	0.23	0.07	0.26	0.25	0.19	—[a]
		3	4	0.00	0.00	0.33	0.12	0.55	—[a]
		4	5	0.02	0.00	0.62	0.26	0.09	0.00
		5	1	0.00	0.00	0.75	—[a]	0.11	0.14
S	WP	1	7	0.08	0.03	0.54	0.07	0.09	—[a]
		2	4	0.04	0.01	0.68	0.12	0.15	—[a]
		3	8	0.13	0.00	0.29	0.21	0.37	—[a]
		4	10	0.01	0.01	0.63	0.26	0.08	0.01
		5	1	0.00	0.00	0.50	—[a]	0.00	0.00

[a]Organism was not present in the plankton samples.

TABLE 4. Differences (ANOVA) in preference values (Manly/Chesson index) of prey consumed by age 0 white perch and yellow perch in 1986 (pooled data) and 1987 (by trial) experiments. LEP = *Leptodora*, DAP = *Daphnia*, CYC = cyclopoid copepods, CAL = calanoid copepods, EUB = *Eubosmina*, BYT = *Bythotrephes*, OST = ostracods. NS = not significant ($p > 0.05$).

Trial(s)	LEP	DAP	CYC	CAL	EUB	BYT	OST
			1986				
1, 2, 3	0.0239	NS	NS	—	NS	—	NS
			1987				
1	NS	NS	NS	NS	0.0347	—[a]	—[a]
2, 3	NS	NS	NS	NS	NS	—[a]	—[a]
4	0.0294	NS	NS	NS	0.0038	—[a]	—[a]
5	NS	NS	NS	—[a]	0.0299	NS	—[a]

[a]Organism was not present.

Eubosmina, where yellow perch ate more than white perch (Table 4). From the pooled 1986 data and the 1987 trials, there were no differences between the two species in the array of organisms eaten (MANOVA, $p > 0.01$).

Discussion

Our results indicate that age 0 white perch and yellow perch are equally capable of feeding on zooplankton, which is important to know in evaluating white perch – yellow perch interactions in the field. There were no prey selectivity differences in single or combined assemblages, within a species, or between species. This laboratory situation could be extrapolated to the field, if the prey resources of these fishes are not limiting. Although prey depletion (*Leptodora*, 1986) was possible in the experiments, which presents problems in calculating preferences (Chesson 1983), usually many organisms were not eaten. In addition to use, we were interested in examining the size and species of prey both fishes ate. According to the size-efficiency hypothesis (Brooks and Dodson 1965), an animal should optimize its energy intake and increase its fitness (optimal foraging theory; Charnov 1976). Werner and Hall (1974) found that prey were eaten as encountered at low densities, while size selectivity operated when densities were high. Also, animals should be more selective when satiated (Emlen 1966).

We found that white perch were generally not eating the largest, low-density prey (*Leptodora* in both years and *Bythotrephes* in 1987). However, yellow perch marginally selected for *Leptodora* in 1986. Both species generally selected the most numerous prey in 1986, but in 1987 consumed cyclopoid and calanoid copepods more than the most numerous prey, *Leptodora* and *Daphnia*. Hansen and Wahl (1981) found from field collections that yellow perch ate the smaller prey of those sizes available, even though the fish were capable of ingesting the larger sizes. Their explanation was that young fish are less successful in capturing large prey. Mills et al. (1984) conducted laboratory feeding experiments with young yellow perch and zooplankton prey and also found the fish eating smaller organisms. However, their data suggested that yellow perch were capable of capturing the largest daphnids and should elect to consume those items. Mills et al. (1986) concluded that yellow perch may digest larger daphnids inefficiently, resulting in consumption of the smaller sizes.

From Mills et al. (1986), Furnass (1979), and Mittelbach (1981), it is evident that young planktivorous fish feed in patterns apparently inconsistent with optimal foraging strategies, which predict that planktivores feed on the largest plankton. However, reduced searching ability, handling efficiency, and ability to detect size differences in prey may affect prey selection by young fish (Mittelbach 1981). In a recent paper, Confer et al. (1990) asserted that young yellow perch select prey based on nutritional quality of the plankton, rather than size. Deviations from expected selectivities in our experiments may be related to these factors.

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Metabolic Organization of a Primitive Fish, the Bowfin (*Amia calva*)

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Singer, T. D., and J. S. Ballantyne. 1991. Metabolic organization of a primitive fish, the bowfin (*Amia calva*). Can. J. Fish. Aquat. Sci. 48: 611–618.

Key enzymes in several metabolic pathways in five tissues were measured in primitive osteichthyan, the bowfin (*Amia calva*), the only living representative of the group of extant fishes most closely allied to the teleosts. Aspects of the metabolism of *Amia* differ from those of most teleosts studied. These differences include detectable levels of β-hydroxybutyrate dehydrogenase in all tissues, possibly a primitive metabolic feature of vertebrates, subsequently lost in most more advanced teleosts. Based on 3-hydroxyacyl CoA dehydrogenase and carnitine palmitoyltransferase activities, lipid metabolism in extrahepatic tissues of bowfin more closely resembles that of an elasmobranch rather than that of a teleost. The overall level of metabolism is lower than most teleosts as indicated by enzyme activities in red muscle and heart. Bowfin plasma nonesterified fatty acid concentrations are lower than most teleosts, but higher than those detected in any elasmobranch. These data suggest that the metabolic organization, especially lipid and ketone body metabolism, at least in part, reflects the evolutionary history of this group.

On a pratiqué des dosages d'enzymes essentielles de plusieurs voies métaboliques dans cinq tissus d'un ostéichtien primitif, le poisson-castor (*Amia calva*) seul représentant vivant du présent groupe de poissons les plus apparentés aux téléostéens. Par certains aspects, le métabolisme d'*Amia* diffère de celui de la plupart des téléostéens étudiés. Il y a notamment la concentration détectable de β-hydroxybutyrate déshydrogénase dans tous les tissus, qui peut être une caractéristique métabolique primitive des vertébrés qui se serait perdue chez la plupart des téléostéens les plus évolués. D'après la mesure de l'activité de la 3-hydroxyacyl CoA déshydrogénase et de la carnitine palmitoyltransférase, on constate que le métabolisme des lipides dans les tissus extrahépatiques du poisson-castor s'apparente davantage à celui d'un élasmobranche qu'à celui d'un téléostéen. Le niveau métabolique d'ensemble est inférieur à celui de la plupart des téléostéens comme il est indiqué par l'activité enzymatique dans le muscle volontaire et dans le muscle cardiaque. Chez le poisson-castor, la concentration des acides gras libres du plasma est inférieure à celle de la plupart des téléostéens, mais elle est supérieure à celle de la plupart des élasmobranches. Ces résultats indiquent que l'organisation métabolique, notamment celle du métabolisme des cétones et de celui des lipides, est un reflet, du moins partiel, de l'évolution de ce groupe.

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Recent studies (Zammit and Newsholme 1979; Ballantyne et al. 1987; Singer and Ballantyne 1989) indicate marked differences between the metabolic organization of the phylogenetically ancient elasmobranchs and the more recent teleosts. There are three main differences. (1) There is reduced extrahepatic lipid oxidation in marine (Zammit and Newsholme 1979; Driedzic and Hart 1984; Ballantyne and Moon 1986) and freshwater elasmobranchs (Singer and Ballantyne 1989) compared with teleosts. (2) Most teleosts lack detectable levels of the enzyme β-hydroxybutyrate dehydrogenase (β-OHBDH) required for oxidation of the ketone body β-hydroxybutyrate, while substantial levels of this enzyme occur in freshwater (Singer and Ballantyne 1989) and marine elasmobranchs (Zammit and Newsholme 1979). The lack of β-OHBDH in the species of teleosts examined by Zammit and Newsholme (1979) was accompanied by the complete absence of β-hydroxybutyrate in the blood compared with elasmobranchs. (3) Concentrations of plasma nonesterified fatty acids (NEFA) are 10 times lower in elasmobranchs than in teleosts (Zammit and Newsholme 1979).

The metabolic differences between the more "primitive" elasmobranchs and the "advanced" teleosts suggest that certain osteichthyans which occupy intermediate phylogenetic positions may have a metabolic organization of lipid/ketone body oxidation that is intermediate between those of the teleost and the elasmobranch. Such is the case for the lake sturgeon (*Acipenser fulvescens*), a member of an ancient group of osteichthyans, the chondrosteans, positioned phylogenetically between elasmobranchs and teleosts (Singer et al. 1990). In some respects, sturgeon metabolism on the one hand resembles that of the teleosts: the tissue distribution of the enzymes involved with fatty acid oxidation and transport is similar to the teleosts, although the enzymes occur at reduced levels; plasma levels of NEFA of the sturgeon are clearly higher than those measured in any elasmobranch yet lower than most teleosts. On the other hand, the sturgeon is much like the elasmobranch biochemically, including detectable levels of β-OHBDH in its tissues (Singer et al. 1990). It therefore seems that evolutionary factors play an important role in the metabolic organization of primitive fish such as the sturgeon.

The bowfin (*Amia calva*), a bony nonteleostean fish, has a common ancestor with the sturgeon dating from some 360 million yr ago (Boreske 1974). The bowfin is a uniquely North American fish occupying an evolutionary position intermediate between the elasmobranchs and the teleosts. Being the only living representative of the family Amiidae, it has been the

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focus of a variety of phylogenetic studies (Patterson 1973; Jarvik 1980; Schultze and Wiley 1984). Fossil members of this family from the Tertiary period are known from North America, Europe, and Asia (Boreske 1974). The first holosteans, forms similar to the living *Amia*, appeared 200 million yr ago and are thought to have given rise to the present-day teleosts (Becker 1983).

The bowfin possesses a peculiar mixture of primitive and advanced anatomical and behaviourial features which distinguish it from the modern teleosts. The primitive characteristics retained by *Amia* include a skeleton composed of both bone and cartilage and a shark-like, abbreviated, heterocercal caudal fin (Scott and Crossman 1973). The advanced features include a respiratory swimbladder used to augment oxygen uptake under hypoxic conditions (Randall et al. 1981), an egg transport system similar to that of elasmobranchs and terrestrial vertebrates (Becker 1983), and a highly specialized reproductive habit in which parental care plays a conspicuous role (Scott and Crossman 1973). Examination of the metabolism of this unusual primitive osteichthyan has been confined to single enzyme (carabamyl phosphate synthetase) (Cvancara 1974) or single tissue (gill) (Mommsen 1984) studies, while its metabolic organization has yet to be examined. As our previous investigations of the sturgeon (Singer et al. 1990) suggest, the bowfin may also have a metabolic organization different from that of teleost fish.

In particular, we examined the capacity of selected tissues of the bowfin for lipid and ketone body oxidation. The activities of various enzymes of intermediary metabolism, particularly those involved in the metabolism of lipids and ketone bodies, were measured. An important question is whether β-OHBDH is found in the group of extant fishes most closely allied to the teleosts (Amiiformes). Levels of plasma individual NEFA were measured as an index of the reliance of specific fatty acids.

Materials and Methods

Experimental Animals

Bowfin were obtained from a commercial fisherman from Lake Erie and held at the Marine Biology Laboratory, University of Guelph, in freshwater at 10 (±1.0)°C for 3 mo prior to use. Animals were fed ad libitum on chopped herring, chopped live worms, and a commercial salmonid diet daily (Diet 84G, Martin Feed Mills Ltd, Elmira, Ont.) and were observed to feed. Fish weighed between 414 and 568 g.

Tissue Preparation

Animals were killed by a blow to the head and tissues were removed rapidly and placed in 5 volumes of ice-cold 50 mM imidazole buffer, pH 7.4, at 10°C. All preparative procedures were carried out at 4°C. Tissues were homogenized using a Polytron PT10 unit (Kinematica Gmbh., Luzurn, Switzerland) for three bursts lasting 10 s each time. Homogenates were centrifuged at 18 200 *g* for 20 min at 4°C and an aliquot of the resulting supernatant was used in enzyme assays. In the cases of carnitine palmitoyltransferase (CPT), carnitine octanoyltransferase (COT), carnitine acetyltransferase (CAT), and citrate synthase (CS), Triton X-100 was added to the homogenate to make a 0.2% solution, which was then sonicated using a Megason PA-300 unit (Ultrasonic Instruments International, Farmingdale, NY) with three bursts of 10 s each at the highest setting prior to conducting the enzyme assay.

Enzyme Assays

Maximal enzyme activities were determined using a Varian DMS 100 UV-Visible spectrophotometer (Varian Canada Inc., Georgetown, Ont.) equipped with a thermostated cell changer maintained at 10 (±0.1)°C with a Haake D8 circulating water bath (Haake Buchler Instruments Inc., Saddlebrook, NJ). Reaction rates of most enzymes were determined by change in absorbance of NADH or NADPH at 340 nm (millimolar extinction coefficient ϵ_{340}, 6.22). CS and the carnitine acyltransferases were monitored at 412 nm using 5,5′-dithiobis 2-nitrobenzoic acid (DTNB) (millimolar extinction coefficient ϵ_{412}, 13.6) Acetoacetyl-CoA thiolase (ACoAT) was measured at 313 nm using the method of Williamson et al. (1971) (millimolar extinction coefficient ϵ_{313}, 20.5). Succinyl coenzyme-A ketotransferase (SKT) was monitored at 310 nm (millimolar extinction coefficient ϵ_{310}, 11.9) using the method of Moon and Mommsen (1987). Enzyme activities were expressed as units per gram of wet tissue weight where 1 unit equals 1 μmol of substrate converted to product per minute.

Conditions of the enzyme assays were optimized with respect to substrate concentration as follows.

Enzymes of lipid catabolism

Carnitine palmitoyltransferase (CPT; EC 2.3.1.21): 50 mM imidazole, pH 8.0, at 20°C, 0.2 mM DTNB, 0.1 mM palmitoyl CoA, 5 mM L-carnitine (omitted for control).

Carnitine octanoyltransferase (COT; EC 2.3.1.21): 50 mM imidazole, pH 8.0, at 20°C, 0.2 mM DTNB, 0.1 mM octanoyl CoA, 5 mM L-carnitine (omitted for control).

Carnitine acetyltransferase (CAT; EC 2.3.1.7): 50 mM imidazole, pH 8.0, at 20°C, 0.2 mM DTNB, 0.1 mM acetyl CoA, 5 mM L-carnitine (omitted for control).

3-Hydroxyacyl CoA dehydrogenase (HOAD; EC 1.1.1.35): 50 mM imidazole, pH 8.0, at 20°C, 0.1 mM NADH, 0.1 mM acetoacetyl CoA (omitted for control).

Enzyme of lipid synthesis

Malic enzyme (ME; EC 1.1.1.40): 50 mM imidazole, pH 7.4, at 20°C, 1.0 mM $MgCl_2$, 0.4 mM NADP, 1.0 mM malate (omitted for control).

Enzymes of ketone body metabolism

β-Hydroxybutyrate dehydrogenase (β-OHBDH; EC 1.1.1.30): 50 mM imidazole, pH 8.0, at 20°C, 0.1 mM NADH, 2 mM acetoacetate (omitted for control).

Succinyl coenzyme-A ketotransferase (SKT; EC 2.8.3.2): 50 mM imidazole, pH 8.0, at 20°C, 5 mM $MgCl_2$, 0.1 mM acetoacetyl CoA, 1 mM succinate (omitted for control).

Acetoacetyl-CoA thiolase (ACoAT; EC 2.3.1.9): 50 mM imidazole, pH 8.0, at 20°C, 5 mM $MgCl_2$, 0.14 mM acetoacetyl CoA, 0.24 mM CoA (omitted for control).

Enzyme of oxidative metabolism

Citrate synthase (CS; EC 4.1.3.7): 50 mM imidazole, pH 8.0, at 20°C, 0.1 mM DTNB, 0.3 mM acetyl CoA, 0.5 mM oxaloacetate (omitted for control).

Enzymes of glycolysis

Hexokinase (HK; EC 2.7.1.1): 50 mM imidazole, pH 7.4, at 20°C, 1 mM glucose, 5 mM $MgCl_2$, 0.16 mM NADP, 2 units of glucose 6-phosphate dehydrogenase (G6PDH), 1 mM ATP (omitted for control).

Phosphofructokinase (PFK; EC 2.7.1.11): 50 mM imidazole, pH 7.4, at 20°C, 10 mM $MgCl_2$, 50 mM KC1, 0.15 mM NADH, 2 mM ATP, 1 unit of α-glycerophosphate dehydro-

genase, 1 unit of triosephosphate isomerase, 1 unit of aldolase, 5 mM D-fructose 6-phosphate (omitted for control).

Lactate dehydrogenase (LDH; EC 1.1.1.27): 50 mM imidazole, pH 7.4, at 20°C, 0.2 mM NADH, 1 mM pyruvate (omitted for control).

Enzyme of gluconeogenesis

Fructose 1,6-bisphosphatase (FBPase; EC 3.1.3.11): 50 mM imidazole, pH 7.4, at 20°C, 15 mM $MgCl_2$, 0.2 mM NADP, 2 units of G6PDH, 10 units of phosphoglucose isomerase, 0.1 mM fructose, 1,6-diphosphate (omitted for control).

Enzymes of amino acid metabolism

Glutamate dehydrogenase (GDH; EC 1.4.1.3): 50 mM imidazole, pH 7.4, at 20°C, 250 mM ammonium acetate, 0.1 mM ethylenediaminetetraacetic acid (EDTA), 0.1 mM NADH, 1 mM ADP, 14 mM α-ketoglutarate (omitted for control).

Alanine aminotransferase (AlaAT; EC 2.6.1.2): 50 mM imidazole, pH 7.4, at 20°C, 200 mM L-alanine, 0.2 mM NADH, 0.025 mM pyridoxal phosphate, 1 unit of LDH, 10.5 mM α-ketoglutarate (omitted for control).

Aaspartate aminotransferase (AspAT; EC 2.6.1.1): 50 mM imidazole, pH 7.4, at 20°C, 7 mM α-ketoglutarate, 0.2 mM NADH, 0.025 mM pyridoxal phosphate, 3 units of malate dehydrogenase, 40.0 mM L-aspartate (omitted for control).

Determination of Plasma Nonesterified Fatty Acids (NEFA)

Blood was drawn into heparinized syringes by caudal puncture before killing the fish. The plasma was obtained by centrifugation of whole blood at 4°C and was stored at −20.0°C until use. NEFA in plasma samples were assayed by the method described in Singer et al. (1990). A gas chromatograph (Hewlett-Packard, HP5890A) fitted with a flame ionization detector (FID) and a DB-225 megabore fused silica column (Chromatographic specialities Inc., Brockville, Ont.) under isothermal conditions (200°C) using helium as a carrier gas (Mahadevappa and Powell 1989) was used to analyze NEFA. Fatty acid methyl esters were identified by comparison of their retention times with a lipid class standard and the absolute amounts of these fatty acids were determined using an internal standard, heptadecanoic acid (17:0).

Chemicals

All chemicals were obtained from Sigma Chemical Co. (St. Louis, MO) and were of the highest purity available. Lipid class standard was obtained from Nu Chek Prep, Inc. (Elysian, MN).

Results

The levels of enzymes of several metabolic pathways in brain, red muscle, heart, kidney, and liver (Table 1) provided a qualitative view of the metabolic organization of the bowfin *A. calva*.

Lipid Metabolism

The activity of HOAD, an enzyme involved in the beta-oxidation of fatty acids, was found in all tissues examined with the greatest activity in the liver. CPT, an enzyme which catalyzes the rate-limiting step in carnitine-dependent oxidation of long-chain fatty acids (McGarry and Foster 1980), was not detected in the heart, although there were low levels in all other tissues examined. COT and CAT activities were present in all tissues examined, with liver and kidney having highest activity for both these enzymes. The heart and red muscle had the highest activity of malic enzyme, an enzyme usually associated with fatty acid synthesis, whereas the liver had the lowest activity of malic enzyme.

Table 2 summarizes the absolute and relative amounts of individual NEFA detected in the plasma of the bowfin. Chain lengths shorter than C:14 were not resolved under our conditions. The total NEFA (C:14 and longer) in plasma of *Amia* amounted to 0.758 $\mu mol \cdot mL^{-1}$. Saturates accounted for the major fatty acids detected and contributed 37% of the total, with palmitic acid (16:0) accounting for 29% of the total NeFA found in the plasma of *Amia*. Monounsaturates accounted for 33% of the total NeFA, with palmitoleic acid (16:1, $n-9$) and oleic acid (18:1,$n-9$) accounting for 12.5 and 19.8% of the total plasma NEFA, respectively. The ratio of $n-3/n-6$ fatty acids in the plasma was 1.87 ± 0.35. The ratio of monoenoic/polyenoic fatty acids was 1.25 ± 0.22.

Ketone Body Metabolism

The ability to metabolize β-hydroxybutyrate, as measured by the activity of β-OHBDH, was detectable in all tissues with the highest levels found in the red muscle and heart. Correspondingly, SKT, an enzyme which catalyzes the transfer of coenzyme A from succinyl coenzyme A to acetoacetate to form acetoacetyl coenzyme A, was also detectable in all tissues, but highest activity was observed in the liver. SKT activity in the heart was not as great as that in the liver. ACoAT, an enzyme which catalyzes the cleavage of acetoacetyl coenzyme A to form acetyl coenzyme A, was detected in all tissues but was highest in the liver and heart.

Oxidative Metabolism

Based on activities of CS, an indicator of the potential for aerobic metabolism, the most aerobic tissue was found to be the heart and the lowest the liver.

Glycolysis

Glycolytic capacity was low based on HK, PFK, and LDH activities. HK and PFK were variable but generally low in all tissues. LDH activity, an indicator of the potential for anaerobic glycolysis, was highest in the red muscle and lowest in the liver.

Gluconeogenesis

Gluconeogenic capacity as determined by FBPase activity, a gluconeogenic enzyme common to most gluconeogenic pathways, was highest in the liver and kidney. The heart showed no detectable levels of FBPase activity.

Amino Acid Metabolism

GDH, which catalyzes the oxidative deamination of glutamate to α-ketoglutarate, had highest activity in the liver followed by the kidney. AlaAT, which transaminates alanine to produce pyruvate, was most active in the liver and least active in the heart. In contrast, AspAT, which transaminates aspartate to oxaloacetate, was more active than AlaAT in all tissues, the heart having the highest activity and the brain having the least.

TABLE 1. Enzyme activities ($\mu mol \cdot min^{-1} \cdot g^{-1}$, means ± SEM, $n = 6$) in selected tissues of the bowfin *A. calva*. Conditions as described in Materials and Methods. ND, not detectable. For all other abbreviations, see text.

Enzyme	Brain	Red Muscle	Heart	Kidney	Liver
Lipid catabolism					
HOAD	0.033 ± 0.008	0.094 ± 0.008	0.103 ± 0.006	0.081 ± 0.011	0.323 ± 0.047
CPT	0.007 ± 0.004	0.009 ± 0.005	ND	0.011 ± 0.009	0.029 ± 0.012
COT	0.003 ± 0.003	0.004 ± 0.004	0.019 ± 0.010	0.141 ± 0.035	0.135 ± 0.009
CAT	0.004 ± 0.002	0.046 ± 0.019	0.006 ± 0.004	0.046 ± 0.026	0.078 ± 0.015
Lipid synthesis					
Malic enzyme	0.041 ± 0.008	0.104 ± 0.012	0.126 ± 0.004	0.043 ± 0.010	0.007 ± 0.003
Ketone body metabolism					
β-OHBDH	ND	0.140 ± 0.050	0.124 ± 0.053	0.024 ± 0.013	0.021 ± 0.007
SKT	0.024 ± 0.017	0.234 ± 0.027	0.680 ± 0.047	0.107 ± 0.014	1.564 ± 0.313
ACoAT	0.176 ± 0.042	0.165 ± 0.037	0.471 ± 0.017	0.267 ± 0.039	2.622 ± 0.172
Oxidative metabolism					
CS	3.365 ± 0.201	2.354 ± 0.111	4.696 ± 0.323	2.576 ± 0.181	0.084 ± 0.013
Glycolysis					
HK	0.546 ± 0.078	0.084 ± 0.012	0.427 ± 0.043	0.788 ± 0.068	0.148 ± 0.024
PFK	0.069 ± 0.013	0.139 ± 0.031	0.103 ± 0.015	0.090 ± 0.017	0.042 ± 0.022
LDH	33.02 ± 3.600	65.05 ± 6.128	51.47 ± 2.953	44.09 ± 1.854	3.504 ± 0.273
Gluconeogenesis					
FBPase	0.004 ± 0.004	0.057 ± 0.010	ND	0.344 ± 0.029	0.782 ± 0.112
Amino acid metabolism					
GDH	ND	0.100 ± 0.035	0.271 ± 0.036	0.940 ± 0.182	1.153 ± 0.268
AlaAT	0.498 ± 0.059	0.216 ± 0.053	0.048 ± 0.039	3.721 ± 0.402	9.545 ± 0.666
AspAT	12.75 ± 0.352	25.49 ± 0.943	28.49 ± 0.809	13.76 ± 0.434	22.35 ± 1.086

TABLE 2. Absolute amounts (means ± SEM, $n = 5$) of individual nonesterified fatty acids in plasma of the bowfin *A. calva*.

Fatty acid	Concentration ($\mu mol \cdot mL^{-1}$)	Percentage by moles
14:0	0.028 ± 0.006	3.68 ± 0.49
16:0	0.214 ± 0.029	29.44 ± 2.09
16:1	0.099 ± 0.023	12.47 ± 1.57
18:0	0.030 ± 0.005	4.03 ± 0.42
18:1 ($n-9$)	0.153 ± 0.028	19.76 ± 1.17
18:2 ($n-6$)	0.049 ± 0.010	6.37 ± 1.05
18:3 ($n-3$)	0.013 ± 0.004	1.65 ± 0.45
18:4 ($n-3$)	0.006 ± 0.003	0.69 ± 0.30
20:1	0.014 ± 0.005	1.75 ± 0.53
20:2 ($n-6$)	0.002 ± 0.002	0.21 ± 0.18
20:4 ($n-6$)	0.035 ± 0.013	4.75 ± 1.46
20:4 ($n-3$)	0.001 ± 0.001	0.14 ± 0.08
20:5 ($n-3$)	0.056 ± 0.013	7.62 ± 1.20
22:3 ($n-3$)	0.003 ± 0.002	0.31 ± 0.17
22:5 ($n-3$)	0.011 ± 0.002	1.51 ± 0.10
22:6 ($n-3$)	0.041 ± 0.008	5.60 ± 0.72
Total	0.758 ± 0.110	100
Total saturates	0.273 ± 0.036	37.16 ± 2.11
Total monoenes	0.267 ± 0.052	33.99 ± 2.82
Total polyenoic	0.219 ± 0.035	28.85 ± 2.17
$n-3$ Polyenoic	0.132 ± 0.024	17.53 ± 1.88
$n-6$ Polyenoic	0.086 ± 0.022	11.33 ± 2.19
$n-3/n-6$	1.87 ± 0.35	1.87 ± 0.35
Monoenes/polyenoic	1.25 ± 0.22	1.25 ± 0.22

Discussion

Lipid Metabolism

Based on HOAD activity, lipid oxidation occurs at low levels in the liver as well as all extrahepatic tissues sampled from *Amia*. HOAD activity was highest in the liver. The extrahepatic tissues of *Amia* had lower levels of HOAD than those reported for teleosts (Ewart and Driedzic 1987; Moyes et al. 1989) and a chondrostean, the lake sturgeon (Singer et al. 1990). In teleosts and sturgeons the extrahepatic tissues, such as heart and red muscle, show high HOAD activity, indicating a reliance of these extrahepatic tissues on lipids as a fuel source. The pattern observed in *Amia*, however, more closely resembles the situation in freshwater (Singer and Ballantyne 1989) and marine (Moon and Mommsen 1987) elasmobranchs, which do not rely on fatty acids as oxidative substrates in extrahepatic tissues.

The extent of oxidation of specific fatty acids can also be assessed by measuring the activity of carnitine acyl transferases. These enzymes catalyze a rate-limiting step in fatty acid oxidation in mammals; long-chain fatty acids that are mobilized from depot triglycerides are esterified to L-carnitine and then transferred by acyltransferases into the mitochondrial matrix where oxidation can occur (see McGarry and Foster 1980 for a review). In fish, carnitine-dependent oxidation of long- and medium-chain fatty acids appears to be more important than carnitine-independent fatty acid oxidation (Bilinski and Jonas 1970; Ballantyne et al. 1989). Two forms of carnitine acyl transferases are commonly measured: (1) CPT specific for long-chain fatty acyl carnitines and (2) COT specific for medium-chain acyl carnitines. In the present study, palmitoyl-CoA (C:16) and octanoyl-CoA (C:8) were used as substrates to assess the levels of CPT and COT, respectively.

CPT activity was detectable but low in brain, red muscle, kidney, and liver of *Amia*. These results are in general agreement with those observed in tissues of elasmobranchs (Zammit and Newsholme 1979; Singer and Ballantyne 1989). Driedzic and Hart (1984) showed that elasmobranch hearts, unlike teleost hearts, were unable to use palmitate as fuel for work but relied on ketone bodies as a fatty acid substitute. The studies of Moyes et al. (1986) and Ballantyne and Moon (1986) indicated that a wide range of acyl carnitines are oxidized by isolated liver mitochondria of the marine elasmobranch *Raja*

erinacea, indicating the presence of CPT and COT in this tissue. The levels of palmitate (16:0)(Table 2) in the plasma of *Amia* are higher than any other NEFA, suggesting that palmitate may be the preferred fuel for lipid oxidation. Sidell et al. (1987) have suggested that CPT may utilize fatty acids other than palmitate; thus the CPT activities which are low in the bowfin may underestimate the true potential for carnitine-dependent fatty acid oxidation of long-chain fatty acids.

COT, the enzyme transferring medium-chain (8:0) fatty acids into the mitochondria, is detectable in all tissues of *Amia*, although levels are low. Ratios of CPT/COT activity vary between tissues; however, COT activity was higher than CPT activity in three of the five tissues examined. This suggests that octanoyl carnitine (8:0) may be as important a substrate for beta-oxidation as long-chain acyl carnitines. Based on the present study, low levels of CPT and COT in certain bowfin tissues compared with those of teleost fishes may be due to (1) substantial carnitine-independent oxidation of certain fatty acids, as has been observed in insects (Stevenson 1968; Chamberlin 1987) and lake trout (charr) (*Salvelinus namaycush*) liver mitochondria at low temperatures (Ballantyne et al. 1989), or (2) carnitine-dependent oxidation of unsaturated fatty acids (Henderson and Tocher 1987).

The relatively low level of lipid oxidation in bowfin tissues appears to be supported by dietary studies of *Amia*. Bowfin have been classified as primarily carnivorous fish (Scott and Crossman 1973). The preferred diet of adult bowfin consists of other fishes, crayfish, and frogs (Stacey 1967) which are high in protein. Such a diet may relate to a lower reliance on fatty acids as a substrate for oxidation.

Malic enzyme activities are highest in the extrahepatic tissues such as the heart and red muscle and lowest in the liver. This is similar to the situation in a marine elasmobranch, *R. erinacea* (Moon and Mommsen 1987). High malic enzyme activities in the liver, for generation of NADPH required for fatty acid synthesis, have been found in teleosts in which the liver is the most lipogenic tissue (Henderson and Tocher 1987). It is unlikely that *Amia* relies on extrahepatic tissues for de novo fatty acid synthesis. The malic enzyme activities observed may be more closely associated with amino acid metabolism (Moreadith and Lehninger 1984) rather than with lipid synthesis. This mechanism provides a self-sustaining supply of two carbon units via pyruvate for the oxidation of four carbon units derived from amino acids (Nagel et al. 1980). The low levels of malic enzyme in bowfin suggest that lipid synthesis may occur through citrate lyase rather than malic enzyme (Nagel et al. 1980).

Plasma Nonesterified Fatty Acids (NEFA)

Plasma NEFA are the most metabolically active form of lipid in the blood of vertebrates and indicate the extent to which fatty acids are utilized as a source of fuel (Henderson and Tocher 1987). In fish, plasma NEFA represent the mobilized fatty acids from liver and/or adipose tissue through the action of various lipases. A precise determination of individual NEFA in fish plasma, therefore, is helpful for understanding the turnover (mobilization for oxidation or as eicosanoid precursors) of various fatty acids.

A few studies have measured the total NEFA content in fish plasma using inaccurate, colourimetric assays (Larrson and Fange 1977; Zammit and Newsholme 1979; Plisetskaya 1980; Moon 1983; Black and Love 1986). The colourimetric methods most frequently employed are not suitable for measurement of individual fatty acids and may underestimate total plasma NEFA but are adequate for comparisons within any single method. The method employed in the present study allows quantitative determination of individual NEFA in plasma in a simple one-step reaction (Singer et al. 1990). Zammit and Newsholme (1979), using the colourimetric assay of Duncombe (1963), surveyed NEFA in teleosts and elasmobranchs and found that teleosts had 10-fold higher concentrations of plasma NEFA than did elasmobranchs. A similar trend was apparent in two other surveys of NEFA in plasma including elasmobranchs and teleosts (Larsson and Fange 1977; Fellows et al. 1980). Comparing plasma NEFA levels using the method in this study, it was found that lake charr and Arctic charr (*Salvelinus alpinus*) have total plasma NEFA levels four to five times those of *Amia* (T. D. Singer and J. S. Ballantyne, unpubl. obs.), suggesting that *Amia* has plasma NEFA levels intermediate between elasmobranchs and teleosts. *Amia*, unlike some teleosts, has a low percentage of plasma polyunsaturated long-chain fatty acids. The high concentration of saturated fatty acids in the plasma NEFA may reflect the composition in depot triglycerides although these were not measured in the present study. The high absolute levels of long-chain fatty acids (arachidonic acid (AA), 20:4 ($n-6$), eicosapentaenoic acid (EPA), 20:5 ($n-3$), docosahexaenoic acid (DHA), 22:6 ($n-3$)) in the plasma may indicate a high turnover of eicosanoids in *Amia*. Correspondingly the high absolute levels of AA, 20:4 ($n-6$) indicates that $N-6$ fatty acids may be more important as eicosinoid precursors than $n-3$ fatty acids. A review by Bell et al. (1986) indicates that such fatty acids may be used in fish as they are in mammals, for metabolic conversion to eicosanoids. The low value for the $n-3/n-6$ ratio, normally associated with herbivorous teleosts, is at variance with the diet fed during the experiment as well as *Amia*'s natural high-protein diet. This ratio may not apply to nonteleost fish such as *Amia*.

The wide range in levels of total plasma NEFA observed in fish (absence in elasmobranchs; high levels in teleosts and intermediate levels in sturgeon and bowfin) may be directly correlated with the presence of serum albumin. Albumin is known to transport free fatty acids mobilized from lipid reserves in mammals. Recently an albumin-like protein capable of binding and transporting free fatty acids has been found to exist in the plasma of salmonids (Davidson et al. 1988). A survey of plasma fatty acid binding proteins in elasmobranchs and teleosts by Fellows and Hird (1981) revealed their absence in elasmobranchs. The levels of fatty acids reported here (>0.75 mM) far exceed the solubility of long-chain fatty acids (Windholz 1983). Thus it is likely that *Amia* possesses an albumin-like fatty acid carrier protein and like the teleosts (Zammit and Newsholme 1979) has developed a specific lipid storage tissue and the ability to mobilize and transport NEFA to other tissues.

Ketone Body Metabolism

The bowfin has detectable levels of β-OHBDH in all tissues, with red muscle and heart showing the highest levels, 0.140 and 0.124 units·g^{-1}, respectively, in any nonelasmobranch fish examined to date. This contrasts with the absence of β-OHBDH in most teleosts (Zammit and Newsholme 1979; Driedzic and Hart 1984; T. D. Singer and J. S. Ballantyne, unpubl. obs.) except for a single finding of 0.05 units·g^{-1} detected in cod heart (Hansen and Sidell 1983). Elasmobranchs may rely on ketone bodies generated in the liver from lipid stores as an

important fuel substitute for fatty acids in some extrahepatic tissues (Driedzic and Hart 1984; Ballantyne et al. 1987). Siddell and Driedzic (1985) calculated that carbohydrates and ketone bodies supplied the capacity for regeneration of ATP in heart of elasmobranch whereas carbohydrates and fatty acid oxidation provided teleosts with their energy-generating capacity. Another primitive fish, the sturgeon, has been shown to possess β-OHBDH (Singer et al. 1990). The ability to use β-hydroxybutyrate may be a primitive feature retained from ancient vertebrate ancestors of both elasmobranchs and primitive osteichthyans like *Amia* (present study) and the sturgeon (Singer et al. 1990) but subsequently lost in most teleost fishes.

In the teleosts, usually regarded as 'advanced' or specialized, phylogenesis was accomplished by reducing the amount of genetic material, especially repetitive DNA sequences (Hinegardner 1976a). As a consequence, teleost cells contain generally small amounts of DNA, as low as 1 pg·nucleus^{-1} (Hinegardner and Rosen 1972). Haploid amounts of DNA in *Amia* are reported to be less than 3 pg, while *Acipenser transmontanus*, a sturgeon, has a DNA content of 5.1 pg and all chondrichthyans except for *Hydrolagus* sp. have a DNA content above 3.4 pg (Hinegardner 1976b). There may be metabolic correlates of these differences in DNA content. The presence of β-OHBDH is widespread in vertebrates except for most teleosts (Beis et al. 1980; Hansen and Sidell 1983). It is possible that one consequence of the reduction of genetic material in the teleosts is an inability to express β-OHBDH in any tissue. Thus the teleosts may have had to rely directly on lipids as a main energy source for extrahepatic tissues rather than on β-hydroxybutyrate derived from lipid oxidized in liver. A survey for the presence of β-OHBDH at the molecular level as well as a more complete survey of the presence of this enzyme, based upon enzyme activities, in other primitive fishes is required to address this problem more fully.

The levels of other enzymes of ketone body metabolism were detected in all tissues examined in *Amia*. SKT levels in *Amia* are similar to those reported for the marine elasmobranch *R. erinacea* (Moon and Mommsen 1987). The liver followed by red muscle and heart have the highest level of SKT, suggesting that ketone bodies play an important role in the oxidative metabolism of these tissues. Levels of ACoAT are lower than those reported for both teleosts and elasmobranchs (Beis et al. 1980; Singer and Ballantyne 1989) yet are similar to the sturgeon (Singer et al. 1990).

Oxidative Metabolism

Overall levels of CS in *Amia* were two to five times lower than in most teleosts studied to date (Suarez et al. 1986; Ewart and Driedzic 1987; Sidell et al. 1987; Moyes et al. 1989). CS levels are comparable with the marine elasmobranch *R. erinacea* (Moon and Mommsen 1987) and are slightly lower than the lake sturgeon in all tissues except the brain (Singer et al. 1990). Johansen et al. (1970) reported that *Amia* is inactive and is exclusively a water breather at 10°C (the temperature for the current study). At higher temperatures, *Amia* becomes more active and the importance of air breathing increases. Further studies are required to determine the compensatory effect of temperature on oxidative as well as other enzyme systems.

Glycolysis

The highest HK levels are found in the kidney followed closely by brain and heart. HK and PFK levels are low in all tissues compared with values reported in teleosts (Driedzic and Stewart 1982; Moon 1983; Ewart and Driedzic 1987; Sidell et al. 1987). HK levels are similar to those found in the marine elasmobranch *R. erinacea* by Moon and Mommsen (1987); PFK levels are lower. *Amia* has the highest PFK levels in the red muscle although these are low in comparison with those in teleost fish. The low levels of these enzymes suggest that carbohydrates are not the preferred fuel in most tissues.

Anaerobic capacity of the red muscle is not high compared with some teleosts based on LDH levels. *Amia* has a red muscle LDH activity of 65.05 ± 6.128 units·g^{-1} which is similar to another primitive bony nonteleost, the lake sturgeon, in which red muscle LDH levels were measured at 10°C to be 39.96 ± 8.670 units·g^{-1} (Singer et al. 1990). Similarly, Moon and Mommsen (1987) found low levels in the red muscle of the marine elasmobranch *R. erinacea*, with values of 59.34 ± 4.16 units·g^{-1} when measured at 10°C. In contrast, LDH levels are considerably higher in the red muscle of teleosts examined to date. For example, LDH levels in the red muscle of carp (*Cyprinus carpio*) (Moyes et al. 1989), goldfish (*Carassius auratus*) (van den Thillart and Smit 1984), and chain pickerel (*Esox niger*) (Kleckner and Sidell 1985) ranged from 756 ± 132 units·g^{-1} in the carp to 297.96 ± 34.06 units·g^{-1} in the chain pickerel. This suggests that *Amia*'s ability to tolerate hypoxic water is less the result of some biochemical reorganization than its ability to breath air (Johansen et al. 1970; Daxboeck et al. 1981; Randall et al. 1981). *Amia* has been reported to estivate without water (Dence 1933; Neill 1950) although this has been challenged by McKenzie and Randall (1990).

Gluconeogenesis

Elevated levels of FBPase activity in the liver and kidney compared with all other tissues indicate that these tissues are the major gluconeogenic sites as occur in marine elasmobranchs (Moon and Mommsen 1987), freshwater elasmobranchs (Singer and Ballantyne 1989), sturgeon (Singer et al. 1990), as well as many teleosts (see Suarez and Mommsen 1987 for a review). As with other carnivorous fish, amino acids may be the preferred metabolic precursors for gluconeogenesis in *Amia*.

Amino Acid Metabolism

Based on the levels of GDH, AlaAT, and AspAT, *Amia* can utilize amino acids as oxidative substrates. The potential to utilize glutamate and alanine is highest in the kidney compared with other tissues. Comparison with a teleost, the goldfish, indicates similar enzyme profiles, with highest activities in the red muscle and lowest in the liver (Van Waarde 1981). This trend is not observed with the other enzymes of amino acid metabolism. Malic enzyme levels which are highest in heart and red muscle may play a role in amino acid oxidation. More specifically, malic enzyme may be important in glutamine metabolism, as found by Moreadith and Lehninger (1984) in tumour cell mitochondria. Two amino acids, glutamine and proline, have been found to be important substrates in *Amia* red muscle mitochondria (Chamberlin et al. 1991). Further investigations are required to address the role of malic enzyme in amino acid metabolism of fishes.

Evolutionary Considerations

As the only living representative of the family Amiidae, *Amia* has been extensively studied anatomically and placed in an

intermediate position between teleosts and elasmobranchs. The present study indicates that the metabolic organization of *Amia* is also intermediate between that of the elasmobranchs and the teleosts. This is most evident in terms of its ability to utilize lipids and ketone bodies as substrates in the tissues studied. The reduced lipid metabolism in extrahepatic tissues of *Amia* is quite similar to that in elasmobranchs. Our most important discovery, however, is the extent to which *Amia* is able to metabolize β-hydroxybutyrate, in contrast with the lack of this capacity in most teleosts. It is possible that presence of an active form of the enzyme β-OHBDH is a primitive metabolic feature of vertebrates, subsequently lost in most teleosts with a reduction of genetic material. Results from this and a previous study have shown *Amia* to be less closely allied metabolically with the teleosts than the sturgeon. Despite this, the present study supports the contention that aspects of the metabolic organization of *Amia* are related to its evolutionary history.

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Models of the Fish Yield from Lakes: Does the Random Component Matter?[1]

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Generalized linear models were used to investigate the sensitivity of paramater estimates to choice of the random error assumption in models of fisheries data. We examined models of fish yield from lakes as a function of (i) Ryder's morphoedaphic index, (ii) lake area, lake depth, and concentration of dissolved solids, and (iii) fishing effort. Models were fit using a normal, log-normal, gamma, or Poisson distribution to generate the random error. Plots of standardized Pearson residuals and standardized deviance residuals were used to evaluate the distributional assumptions. For each data set, observations were found to be consistent with several distributions; however, some distributions were shown to be clearly inappropriate. Inappropriate distributional assumptions produced substantially different parameter estimates. Generalized linear models allow a variety of distributional assumptions to be incorporated in a model, and thereby let us study their effects.

Des modèles linéaires généralisés ont été appliqués à l'examen de la sensibilité des estimations des paramètres au choix de l'hypothèse relative à l'erreur aléatoire dans les modèles de données sur les pêcheries. Nous avons examiné des modèles de rendement en poisson de certains lacs en fonction de 1) l'indice morpho-édaphique de Ryder, 2) la superficie du lac, la profondeur du lac et la concentration des matières en suspension et 3) l'effort de pêche. Les modèles ont été ajustés selon une distribution normale, logarithmique-normale, gamma ou de Poisson de manière à produire l'erreur aléatoire. Des graphiques de résidus de Pearson centrés et réduits et de résidus centrés et réduits de la somme des carrés d'écarts à la moyenne ont servi à l'évaluation des hypothèses associées à la distribution. Pour chaque ensemble de données, il a été montré que les observations étaient conformes à plusieurs distributions; cependant, il a été montré aussi que certaines des distributions n'étaient pas du tout appropriées. Les hypothèses relatives à ces dernières ont conduit à des estimations des paramètres qui étaient substantiellement différentes des autres. Les modèles linéaires généralisés permettent l'incorporation d'une bonne variété d'hypothèses relatives aux distributions et ainsi, l'étude de leurs effets.

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Formal models play an important role in fisheries research. The number of explicitly stated equations in this journal increased from roughly 14 per 100 pages in 1978 to 25 per 100 pages in 1988. The emphasis in modeling has been on determining the systematic part of the model (i.e. the appropriate explanatory variables and the model's functional form), while the random component (i.e. the random error term) has received little attention. The analysis of formal models has usually assumed normally distributed data, despite the fact that many data sets in fisheries research are not normally distributed. Nonparametric approaches (e.g. robust regression) or transformations of the dependent variable can be used with non-normally distributed data. However, transformation restricts the functional form of the model to be linear on the transformed scale, while nonparametrics result in a less powerful analysis because no knowledge of the statistical distribution is used. Nelder and Wedderburn (1972) developed a maximum likelihood approach for fitting linear models to observations that follow a normal, binomial, Poisson, or gamma distribution (amongst others). Their approach, generalized linear models, has been applied with increasing frequency in biological and medical research. The first text on the subject (McCullagh and Nelder 1983) received more than 300 citations within 5 yr of its publication (Institute for Scientific Information 1985–89).

[1]Ocean Science Centre Contribution 80.

We used generalized linear models to evaluate the extent to which the choice of random distribution can affect parameter estimates in the deterministic component of models of fish yields. Models were fit using data published in the literature.

Generalized Linear Models

Consider a set of observations y_i, $i = 1,\ldots,n$, to be realizations of a random variable Y with expected value (i.e. mean) μ and a distribution belonging to the exponential family. The exponential family includes the normal, Poisson, and gamma distributions amongst others (see, for example, Cox and Hinkley 1974 or Silvey 1975). The deterministic component, or linear predictor, in the model is of the form

$$(1) \quad \eta = \sum_{j=1}^{p} \beta_j x_j$$

where the x_j are p explanatory variables and the β_j are parameters that may or may not be known. The link function $\eta = \mu$ relates the mean of the response variable Y to the linear combination of the x_j and may be any monotonic differentiable function. Common choices of η include logarithmic, reciprocal, and square root forms.

Choice of the link function does not affect the assumptions surrounding the distribution of Y, unlike in the case of trans-

formations used in least-squares methods. Use of the link function permits analysis of a variety of models, as opposed to the single model generated by a transformation applied to produce normal errors. When Y is normally distributed with constant variance σ^2, and $\eta(Y) = Y$, the generalized linear model corresponds to the classical linear model with normal errors.

Nelder and Wedderburn (1972) provided a theoretical development of generalized linear models. McCullagh and Nelder (1989) gave an expanded treatment including the extension to quasi-likelihood theory and numerous worked examples. The Numerical Algorithms Group distributes the software package GLIM which implements these methods (Payne 1986).

Models of Fish Yield

Ryder (1965) compiled data on fish yield (pounds per acre per year), lake area (square miles), mean depth (feet), and total dissolved solids (parts per million) from 23 moderately to heavily fished lakes ranging in size between 1 mi^2 (Lake Hemming) to 31 820 mi^2 (Lake Superior). The data have been analyzed using several deterministic models relating fish yield to lake morphometry and chemistry (Ryder 1965; Schneider and Haedrich 1989). Ryder's (1965) original model is given by

$$(2) \quad H = e^c \mathrm{MEI}^b$$

where, after conversion to metric units, H is production (kilograms per hectare per year) and MEI (parts per million per metre) is the ratio of total dissolved solids (parts per million) divided by the average depth (metres). The parameters b and c are estimated from the data. Ryder (1965) assumed that the logarithm of H was normally distributed and hence fit

$$(3) \quad \log(\mathrm{H}) = c + b \log(\mathrm{MEI})$$

using least-squares methods with normal errors.

Schneider and Haedrich (1989) reanalyzed Ryder's (1965) data using the more general model

$$(4) \quad Q = e^g A^h D^j T^k$$

where e is the base of the natural logarithm, Q is yield of fish (kilograms per year), D is mean lake depth (metres), and T is dissolved solids (parts per million). Ryder (1965) reported values of both D and T; Q is the product of two other reported variables: production H (kilograms per hectare per year) and surface area A (hectares). The parameters g, h, j, and k were estimated from the data. Schneider and Haedrich (1989) assumed that the logarithm of Q was normally distributed and fit

$$(5) \quad \log(Q) = g + h \log(A) + j \log(D) + k \log(T)$$

using least-squares methodology with normal errors.

Jones and Hoyner (1982) presented data from a set of 25 lakes in the midwestern United States and fit the model

$$(6) \quad Y = a + bX$$

where Y is the angler sportfish harvest (kilograms per hectare per year), X is the mean summer chlorophyll a concentration (milligrams per cubic metre), and a and b are parameters estimated from the data. Jones and Hoyner (1982) fit the model using least-squares methods and assumed that Y was normally distributed.

Bayley (1988) presented data on 31 African lakes and proposed the model

$$(7) \quad \log(Y + 1) = ai^{0.5} + bi + c$$

where Y is the annual yield of fish (kilograms per hectare per year), i is the fishing intensity (fishermen per square kilometre), and a, b, and c are fitted parameters. The model was originally fit assuming $\log(Y + 1)$ was normally distributed and using least-squares methodology.

Statistical Methods

Generalized linear models were used to investigate the sensitivity of parameter estimates to the distributional assumption made of the dependent variable. We evaluated models using random components that arise from the following assumptions:

Log-normal: the logarithm of the response variable is normally distributed with constant variance σ^2.

Normal: the response variable itself is normally distributed with constant variance σ^2.

Poisson: the response variable is distributed as a Poisson variable and hence its variance, σ^2, is proportional to the mean.

Gamma: the response variable is distributed as a gamma variable and hence its variance, σ^2, is proportional to the square of the mean.

There is a clear difference in how the variances of the normal, Poisson, and gamma distributions are related to their means. In general, the Poisson distribution is associated with counts, the gamma distribution arises where variation is generated by a mixture of heterogeneous processes, and normal errors occur when outcomes arise from independently acting homogeneous processes. The normal distribution is defined for variables taking both positive and negative values and is symmetric about its mean. The Poisson and gamma distributions apply to positive observations only, and the shape of these distributions is skewed. Because the variance of the Poisson and gamma distributions is related to the mean, the scale chosen to express observations (grams versus kilograms, for example) can affect parameter estimates and their standard errors. We have chosen to express fish yields in kilograms and areas in hectares, although other scales are equally possible. For each of the models, plots of the Pearson residuals and deviance residuals were examined to determine whether any of the distributional assumptions were inappropriate.

Standardized Pearson residuals are the differences between the observed and predicted values, standardized to make their variance (theoretically) constant. The form of the standardizing factor depends on the distributional assumption and is given explicitly in McCullagh and Nelder (1989) or Pierce and Schafer (1986). For each model, standardized Pearson residuals were plotted versus the predicted values. If the assumed error distribution is correct, plots of these residuals should show constant variance.

In generalized linear models, the model *deviance* is defined as twice the difference between the unrestricted maximum likelihood and the maximized likelihood for the model in question. The standardized deviance residuals are the signed contribution of each observation to the model deviance, standardized to make their variance constant. These residuals have been shown to follow a normal distribution (Pierce and Schafer 1986), and normal probability plots of these residuals were used as a second test of the model's appropriateness.

The parameter estimates are reported for all distributional assumptions and are then compared in light of the assumptions' plausibility.

TABLE 1. Parameter estimates for Ryder's (1965) model, $H = e^c \text{MEI}^b$, fit using Ryder's data ($n = 23$) with four different distributional assumptions. Residual plots indicated that the normal and Poisson distributions were inappropriate. Standard errors of the estimates are shown parenthetically.

Assumption	c	b
Log-normal	0.32 (0.13)	0.45 (0.06)
Normal	0.65 (0.23)	0.33 (0.08)
Poisson	0.49 (0.25)	0.40 (0.09)
Gamma	0.35 (0.13)	0.46 (0.06)

TABLE 2. Parameter estimates for Schneider and Haedrich's (1989) model, $Q = e^g A^h D^j T^k$, fit using Ryder's (1965) data ($n = 23$) with four different distributional assumptions. Residual plots indicated that the normal and Poisson distributions were inappropriate. Standard errors of the estimates are shown parenthetically. Standard errors less than 0.01 are reported as 0.00.

Assumption	g	h	j	k
Log-normal	1.02 (0.70)	1.03 (0.05)	−0.56 (0.12)	0.29 (0.12)
Normal	−2.90 (2.22)	1.34 (0.16)	−1.06 (0.18)	0.57 (0.29)
Poisson	−1.98 (0.00)	1.32 (0.00)	−0.99 (0.00)	0.38 (0.00)
Gamma	0.75 (0.72)	1.04 (0.05)	−0.59 (0.12)	0.36 (0.12)

Results

Parameter estimates for Ryder's (1965) model (2) showed little change when the distributional assumption was altered (Table 1). Parameter estimates of the MEI exponent (b) were most similar for the log-normal and gamma assumptions, while estimates based on the normal and Poisson were lower. Plots of the Pearson residuals failed to indicate that any of the error assumptions were inappropriate; however, the deviance residuals showed strong departures from normality under the assumption of normally distributed production (H) values and moderate departures from normality under the Poisson assumption. The log-normal distribution (as originally adopted by Ryder (1965)) and the gamma distribution appeared to be most appropriate for production.

Table 2 shows the parameter estimates from Schneider and Haedrich's (1982) model (4) fit to Ryder's (1965) data. Again, parameter estimates from the log-normal and gamma distributions were the most similar, while estimates from the normal and Poisson assumptions sometimes differed substantially. This was most striking in estimates for the exponent (h) of area. The log-normal and gamma assumptions suggested that this exponent is 1 whereas for the normal and Poisson assumptions, it was nearer 4/3. Similarly, estimates of the exponent (j) associated with depth ranged from approximately −1 to −1/2, and estimates of the exponent (k) for dissolved solids ranged from approximately 1/3 to 1/2. The different parameter estimates imply different interpretations of the mechanism generating the data (Peters 1983). Pearson residual plots from the normal and Poisson models did not display constant variance, and the deviance residuals for these models revealed departures from normality. Pearson residuals from the log-normal and gamma distributions displayed constant variance, and the deviance residuals followed a normal distribution. As in the Ryder (1965) model, the appropriate distribution for fish yield appears to be either log-normal or gamma.

As mentioned earlier, the magnitude of the standard errors for the Poisson estimates, relative to the estimates themselves, is entirely dependent on the scale chosen to measure the variables. To confirm this, we modeled fish yield after converting the units of observation to tonnes. Under the Poisson assumption, parameter estimates of h, j, and k did not change, while the standard errors of the estimates increased by a factor of roughly 10^2. Regardless of the magnitude of the standard errors, the estimates from the different distributions suggest different scalings of the relationship between fish yield and the explanatory variables.

TABLE 3. Parameter estimates for Jones and Hoyner's (1982) model, $Y = a + bX$, using Jones and Hoyner's data using three different distributional assumptions. Standard errors of the estimates are shown parenthetically.

Assumption	a	b
All observations included (n = 25)		
Normal	−1.77 (8.32)	2.71 (0.26)
Poisson	−3.25 (2.03)	2.76 (0.10)
Gamma	−7.29 (2.82)	3.02 (0.34)
All observations except Little Prairie, Missouri (n = 24)		
Normal	−7.39 (7.28)	2.83 (0.23)
Poisson	−7.36 (1.70)	2.82 (0.09)
Gamma	−6.93 (1.98)	2.79 (0.25)

TABLE 4. Parameter estimates for Bayley's (1988) model, $\log(Y + 1) = ai^{0.5} + bi + c$, fit using Bayley's data ($n = 31$) with four different distributional assumptions. Residual plots indicated that the normal and Poisson distributions were inappropriate. Standard errors of the estimates are shown parenthetically.

Assumption	a	b	c
Log-normal	6.46 (1.08)	−1.95 (0.45)	−0.77 (0.58)
Normal	7.44 (2.63)	−2.34 (0.87)	−1.18 (1.98)
Poisson	6.60 (0.31)	−2.05 (0.11)	−0.60 (0.21)
Gamma	6.45 (1.07)	−1.99 (0.44)	−0.50 (0.57)

Jones and Hoyner's (1982) model (6) was fit using the normal, Poisson, and gamma distributions for sportfish harvest (Table 3). A logarithmic transformation of sportfish harvest would imply a nonlinear model, and so the log-normal assumption could not be incorporated. Plots of the Pearson and deviance residuals indicated no evidence to reject either the normal or Poisson assumption. For the gamma distribution, residual plots revealed that one observation (Little Prairie, Missouri) was particularly influential in determining the regression equation. The slope estimate (b) varied by roughly 10% amongst the three distributions, although there were substantial differences in the estimates of the intercept (a). Upon removing the observation from Little Prairie, residual plots failed to reveal evidence to reject any of the distributional assumptions, and estimates from the different assumptions were in close agreement for both the slope and intercept parameters.

Finally, we fit Bayley's (1988) model (7) using the data from 31 African lakes as reported in his original paper. After fitting the model using the log-normal, normal, Poisson, and gamma distributions, we found that residuals from the normal model were badly skewed. Parameter estimates from all four distributional assumptions are shown in Table 4. The log-normal, Poisson, and gamma distributions provided a reasonable description of the observed fish yields, and the estimates under these assumptions did not differ substantially.

Discussion

Our analyses show that the choice of the random component can affect parameter estimates substantially, and so does matter with respect to the prediction of fish yields from environmental variables. The more appropriate estimates can be determined from analysis of the residuals.

Substantially different parameter estimates were obtained when different error structures were used with Ryder's (1965) model of fish yield. However, similar estimates were obtained from both of the error models that were appropriate to the data, based on the analysis of residuals. Identical results were obtained using the multiple regression model (Schneider and Haedrich 1989) of the same data. The same two error structures (log-normal and gamma) were judged to be appropriate descriptions of the data for both of the systematic models. This consistency is expected, in that the error structure is assumed with respect to the dependent (response) variable and should not change with changes to the systematic model. Different parameter estimates were also obtained for the different error structures used with Jones and Hoyner's (1982) model; however, more consistent estimates resulted when a highly influential observation was removed. In Bayley's (1988) model of yield as a function of fishing intensity, four distributional assumptions were examined and only one (the normal) appeared to be inappropriate based on the examination of residuals. The other three assumptions (the log-normal, Poisson, and gamma) gave similar estimates for each of the parameters.

In none of the four analyses did a single model of the random component emerge as appropriate. Rather, two or more models were found to be appropriate to each set of data. One model, the gamma distribution, was appropriate for all three data sets. This may be due in part to the flexibility of this distribution, which includes the normal distribution as a special case. Other considerations, including the fact that fish yields are always positive, and that fish yields plausibly result from the action of several heterogeneous rates, point to the gamma distribution as a good choice for describing the random component in models of fish yields. However, more data sets would be needed to substantiate the general utility of the gamma distribution in this application.

Our results illustrate the importance of validating assumptions about the random component because the use of an incorrect random component can alter parameter estimates substantially. Validation of assumptions on a priori grounds, while desirable, is not always possible. For example, simple transformation of units (e.g. grams to kilograms) can change the error structure, unless the error structure is normal and the variance is independent of changes in the mean. Biological considerations can serve, at best, as only a rough guide to choice of a random component. Residual plots may often provide the only means of determining the appropriateness of distributional assumptions.

Explained variance (R^2) has traditionally been used to evaluate alternative models in the fisheries literature (e.g. Hanson and Leggett 1982). The presence of normally distributed residuals, which should logically take precedence over goodness of fit as a criterion in model evaluation, has been included in some recent studies (e.g. Bayley 1988). Explained variance cannot be used to compare models where the random component has been allowed to vary because normal errors assume that the variance of the random component (and hence the goodness of fit) is constant, while other distributions assume that fit is related to the magnitude of the response variable. R^2 reflects a model's assumptions as much as its performance and can only be used to compare models with a normal error structure.

The width of confidence intervals (e.g. Jones and Hoyner 1982; Bayley 1988; Schneider and Haedrich 1989) has been suggested to be important in a management context. That is, a prediction from an equation can give a misleading sense of precision unless accompanied by a statement of precision relative to the predicted value. Bayley (1988) showed that width of confidence interval is not measured by R^2. The width of confidence intervals cannot be used to compare models with different error structures because both the width and shape of confidence intervals depend on the choice of model for the random component. However, maximum and minimum ranges of confidence intervals are readily calculated, and still bear reporting.

Changes to a model's error component can incur substantial changes in the resultant parameter estimates. Our analysis showed that some distributions could readily be identified as inappropriate for describing fish yields, but that no single, uniquely appropriate error structure was discernable within any one set of data. Generalized linear models permit error structure to be evaluated within a comprehensive framework, thereby increasing our ability to model fisheries data accurately.

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Using a Numerical Model of the Northeast Pacific Ocean to Study the Interannual Variability of the Fraser River Sockeye Salmon (*Oncorhynchus nerka*)

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The hypothesis that numerical ocean circulation models could benefit fishery management was tested by first simulating the interannual variability of the northeast Pacific Ocean from 1955 to 1979 with the Bryan–Cox–Semtner ocean model (from the Geophysical Fluid Dynamics Laboratory, Princeton, NJ) and then relating the model output to the interannual variability found in the Fraser River sockeye salmon (*Oncorhynchus nerka*). Empirical orthogonal function (EOF) analysis was first used to condense the model output fields as well as the atmospheric forcing data. Next, the amplitude of the EOF's were regressed with the annual values of the sockeye variables (return migration route and timing, marine survival, and fork length) by stepwise multiple regression, with various time lags between the physical and the sockeye variables. The EOF modes associated with interannual variability (usually mode 2) were more often correlated with the sockeye variables than the other modes thought to contain mainly the seasonal cycle (mode 1) or else noise. The correlations between the physical variables and the sockeye variables were highest in the first and final few months of the sockeye marine life.

L'hypothèse selon laquelle les modèles numériques de la circulation océanique pourraient servir à la gestion des pêches a été vérifiée en simulant la variabilité interannuelle des caractéristiques des eaux du Pacifique nord-est de 1955 à 1979 à l'aide du modèle des océans de Brian–Cox–Semtner (du Geophysical Fluid Dynamics Laboratory, Princeton, NJ) puis en établissant un rapport entre la sortie du modèle et la variabilité interannuelle relevée chez le saumon rouge (*Oncorhynchus nerka*) du fleuve Fraser. Une analyse empirique des fonctions propres orthogonales a servi à résumer les zones de sortie du modèle ainsi que les données atmosphériques de contrainte. Puis on a calculé une régression de ces fonctions et des valeurs annuelles des variables relatives au saumon rouge (circuit et moment de la remonte, taux de survie en mer et longueur à la fourche) à l'aide d'une analyse de régression multiple séquentielle avec divers décalages du temps entre les variables physiques et les variables relatives au saumon rouge. Les modes des fonctions propres orthogonales liés à la variabilité interannuelle (généralement le mode 2) étaient plus souvent en corrélation avec les variables du saumon rouge que les autres modes que l'on croyait contenir principalement le cycle saisonnier (mode 1) ou bien du bruit. Les corrélations entre les variables physiques et les variables du saumon rouge étaient plus importantes au cours des premiers et des derniers mois du cycle vital du saumon rouge en mer.

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Since the pioneering work of Bryan and Cox (1967), three-dimensional numerical ocean circulation models have evolved rapidly alongside their more senior relatives, the atmospheric general circulation models. It is increasingly probable that numerical ocean models may evolve like their atmospheric counterparts into prediction models. If numerical weather prediction benefits many human activities, e.g. agriculture, could not numerical ocean modelling similarly aid fishery management? To test this concept, we ran a numerical model to hindcast the circulation in the northeast Pacific Ocean from 1955 to 1979 and then attempted to relate the simulated interannual variability to the observed variability (in the return migration route and timing, marine survival, and fork length) of the Fraser River sockeye salmon (*Oncorhynchus nerka*).

With an average annual catch value of $60 million to Canadian fishermen and $17 million to U.S. fishermen for the period 1983–86 the Fraser River sockeye is probably the most valuable fishery for British Columbia. The northern diversion rate of this fish (defined as the percentage of adult fish returning to the Fraser River for spawning in its tributaries by going around the northern end of Vancouver Island instead of around the southern end; Fig. 1) shows large interannual variability (Mysak 1986; Groot and Quinn 1987). The Chilko River (a well-monitored tributary of the Fraser River) provides other sockeye time series with interannual variability: the return timing, marine survival, and age 4_2 male sockeye fork length.

After a brief description of the numerical model and its output in the following section, stepwise multiple regression between the model output and the sockeye time series was used

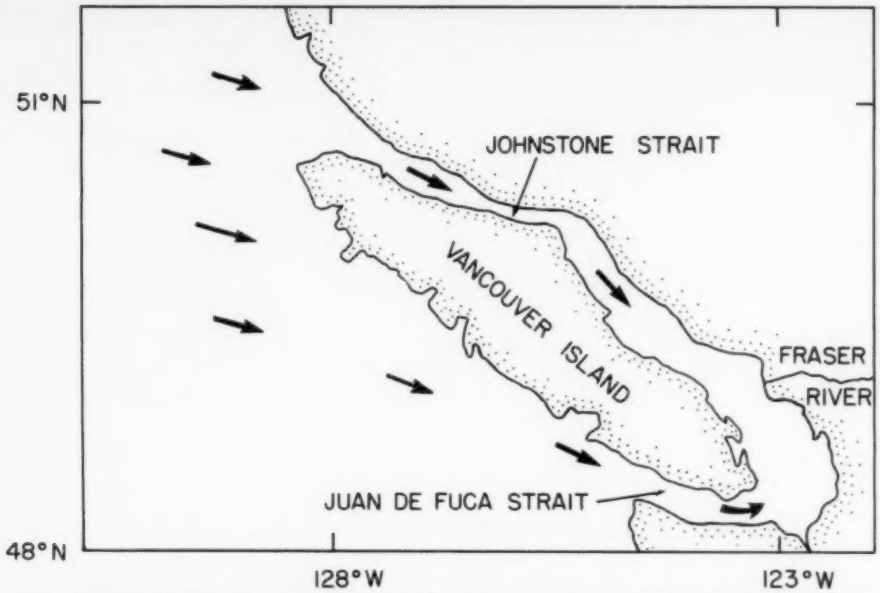

FIG. 1. Schematic diagram showing the two possible return migration routes of the Fraser River sockeye salmon. Approaching the coast from open ocean, the salmon return to the Fraser River via Johnstone Strait to the north or Juan de Fuca Strait to the south.

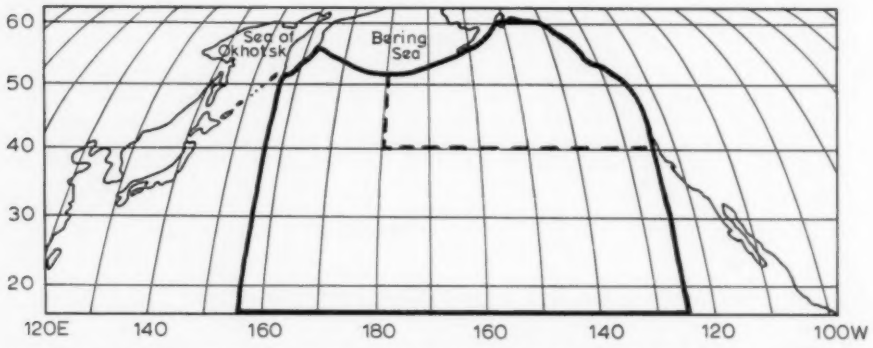

FIG. 2. Map of the North Pacific Ocean, with the model domain bounded by the thick curve. Data in the smaller northeast Pacific region, as bounded by the broken curve, were analyzed by empirical orthogonal functions.

in the third section to connect the physical variability with the fish variability. The implication of our study for future research is discussed in the last section.

Numerical Modelling of the Interannual Variability in the Northeast Pacific Ocean

The Cox (1984) version of the Bryan–Cox–Semtner three-dimensional primitive-equation ocean circulation model, developed originally at the Geophysical Fluid Dynamics Laboratory (GFDL), Princeton, NJ, is used. The model extends from 157°E to 124°W and from 16°N to 60°N (Fig. 2), bounded all around by solid, no-slip walls. There are five vertical levels centred at 10, 60, 200, 800, and 3000 m. The horizontal grid spacing is 1° latitude by 1° longitude from 40°N to 60°N. South of 40°N, the north–south grid spacing gradually broadens to 2° latitude at the southern boundary. The east–west extent of the model is not wide enough to allow the model to follow the actual coastline (Fig. 2) in the western and the southeastern parts of the model. This limitation and the coarser resolution in the southern part of the model were adopted to reduce the extensive computing costs, as we are primarily interested in the higher latitude eastern Pacific region.

The model equations are the fully nonlinear conservation equations governing the changes in momentum, mass, heat, and salt and the equation of state for density. The eddy viscosities in the horizontal and vertical directions are 5×10^3 and 1×10^{-4} $m^2 \cdot s^{-1}$, respectively, while the eddy diffusivities in the two directions are 2×10^3 and 1×10^{-4} $m^2 \cdot s^{-1}$, respectively. For more detailed descriptions of the model, see Hsieh and Lee (1989, 1990).

Using atmospheric data from the Comprehensive Ocean Atmosphere Data Set (COADS) (compiled through the cooperative effort of CIRES, ERL, NCAR, and NCDC), we spun the ocean model up from rest with forcing by the climatological monthly mean observed windstress and surface heat flux (esti-

mated from the difference between the climatological air temperature and the model surface temperature). Due to the lack of surface freshwater flux data, the surface salinity was held constant with time. After 19 yr of spinup, the model reached quasi-equilibrium. We then forced the model using the observed monthly windstress and surface heat flux (by relaxing the model sea surface temperature to the observed air temperature) from 1955 to 1979.

Next, the massive amount of output from the model (25 yr of monthly data) needs to be condensed dramatically before connections with the various sockeye time series can be made. The most efficient method to condense data is the empirical orthogonal function (EOF) analysis, also known as principal component analysis (Preisendorfer and Mobley 1988). In essence, we decompose a variable such as the ocean temperature T, which is a function of both space $\underline{x}$ and time t, into the sum

$$(1) \quad T(\underline{x}, t) = \sum_n a_n(t) e_n(\underline{x})$$

where the e_n's are the spatial orthogonal functions or modes and the a_n's are the time-varying amplitudes of these orthogonal modes. To see how this method condenses the amount of information, we must bear in mind that as the surface temperature field is defined over 2000 grid points, it is a huge data set containing over 2000 time series. But if 95% of the variance of the surface temperature can be described by say the first three modes, then the temporal variation of the surface temperature field is essentially described by three time series (a_1, a_2, and a_3) instead of over 2000 time series!

Hsieh and Lee (1990) described in detail the EOF analysis of the temperature and currents for the upper levels of the model as well as the atmospheric forcing data (the observed windstress and surface air temperature) for the northeast Pacific region in Fig. 2 (using data from every other grid point). The total percentage of variance explained by the first four modes for model surface temperature, air temperature, surface currents, and windstress were respectively 97, 97, 47, and 48%.

From examining the temporal variation of the a_n's, we found that generally the seasonal cycle was most dominant in the first mode, the interannual variability in the second mode, and increasing noise in the higher modes. For example, the first two EOF modes $e_1(\underline{x})$ and $e_2(\underline{x})$ for the model surface temperature are shown in Fig. 3a and 3b, respectively, and their corresponding amplitudes $a_1(t)$ and $a_2(t)$ in Fig. 3c. While a_1 is clearly dominanted by the seasonal cycle, a_2 reveals significant interannual variability, e.g. a_2 rose significantly during the El Niño warm episodes of 1957–58, 1969, and 1976 and less strongly during 1972. The net effect on the surface temperature from the rise in a_2 is to give warmer temperatures in the eastern half of the Gulf of Alaska and cooler temperatures in the western half, as manifested in the pattern of e_2 (Fig. 3b). Such a pattern is in agreement with the EOF analysis of observed sea surface temperature by Weare et al. (1976).

Regression between Physical and Sockeye Variables

The four Fraser River sockeye time series selected for regression with the physical data were the northern diversion (scaled by the logit transformation as in Xie and Hsieh 1989), the Chilko River sockeye return timing (Blackbourn, 1987), marine survival, and age 4_2 male fork length (Blackbourn and Tasaka 1990). The annual values for each of these sockeye variables are shown in Fig. 4.

To relate the model physical variables to the fish variables, we used stepwise multiple regression

$$(2) \quad F = b_0 + b_1 a_n(\text{MayJunJul}) + b_2 a_n(\text{FebMarApr}) + b_3 a_n(\text{NovDecJan}) + \ldots$$

where F denotes one of our four fish time series, a_n one of the EOF amplitude times series of a physical variable (e.g. surface temperature, currents, windstress, and air temperature), and b_m's the regression coefficients. The regression was with physical variables at various 3-mo time lags, e.g. a_n(MayJunJul) denoted the 3-mo average for a_n for the months May, June, July, during or just prior to the fish return, a_n(FebMarApr) denoted the average of a_n for the three previous months, etc., until we reached the early months in the year of the juvenile sockeye entry into the ocean, i.e. 2 yr ago. With so many regression terms, we used stepwise multiple regression (Weisberg 1985) as a systematic procedure to determine which terms were statistically significant enough (according to the F test at the 95% significance level) to be retained in the regression formula. Starting with many terms in the regression formula, this procedure eliminated the terms that failed to meet the significance criterion. This elimination procedure was iterated until convergence to a final regression formula was achieved. The remaining terms (if any) in the final regression formula then indicated which of the a_n's may have exerted an influence on the fish variable during a particular 3-mo interval. Regressions were repeated for the a_n time series of each of the first four modes ($n = 1, \ldots, 4$) for each of the four physical variables (i.e. the air temperature and model surface temperature, windstress and currents).

For the vector quantities, i.e. windstress and currents, the EOF analysis yielded complex a_n's with two components, one lengthening or shortening all the vectors in the EOF mode and the other rotating all the vectors in the mode (Legler 1983). As this effectively caused a doubling of terms in the regression formula when dealing with vector variables, we raised the level of F test to 97.5% in the stepwise multiple regression to compensate for this problem with vector variables. Since we were not sure if May, June, July was the best choice for the first 3-mo interval, we also repeated the regressions with April, May, June, and March, April, May as the starting intervals. Our approach was essentially a "shotgun" approach, i.e. we regressed the sockeye data with every conceivable physical variable at various time lags and collected statistics of the resulting "hits." A very large table or matrix resulted where each entry contained the regression result between a particular sockeye variable and a particular physical variable. Much smaller tables (Tables 1 and 2) were produced by counting the number of "significant" cases over either the rows or columns of this huge matrix, where "significant" cases were defined as cases where the final regression formula (2) after the stepwise elimination procedure still retained at least one of the b_m's ($m = 1, 2, \ldots$).

Clearly, the correlations were relatively low (Table 1), and despite having passed the F test, the numerous cases we tried 9meant that some of the "significant" cases could still have arisen from chance. With this caveat, we nevertheless noted that the second mode of all the physical variables had more "significant" cases than the other modes. This would be expected if mode 1 largely contained the seasonal cycle, mode 2, the interannual variability, and modes 3 and higher, increasing amounts of noise. If modes 3 and 4 were regarded

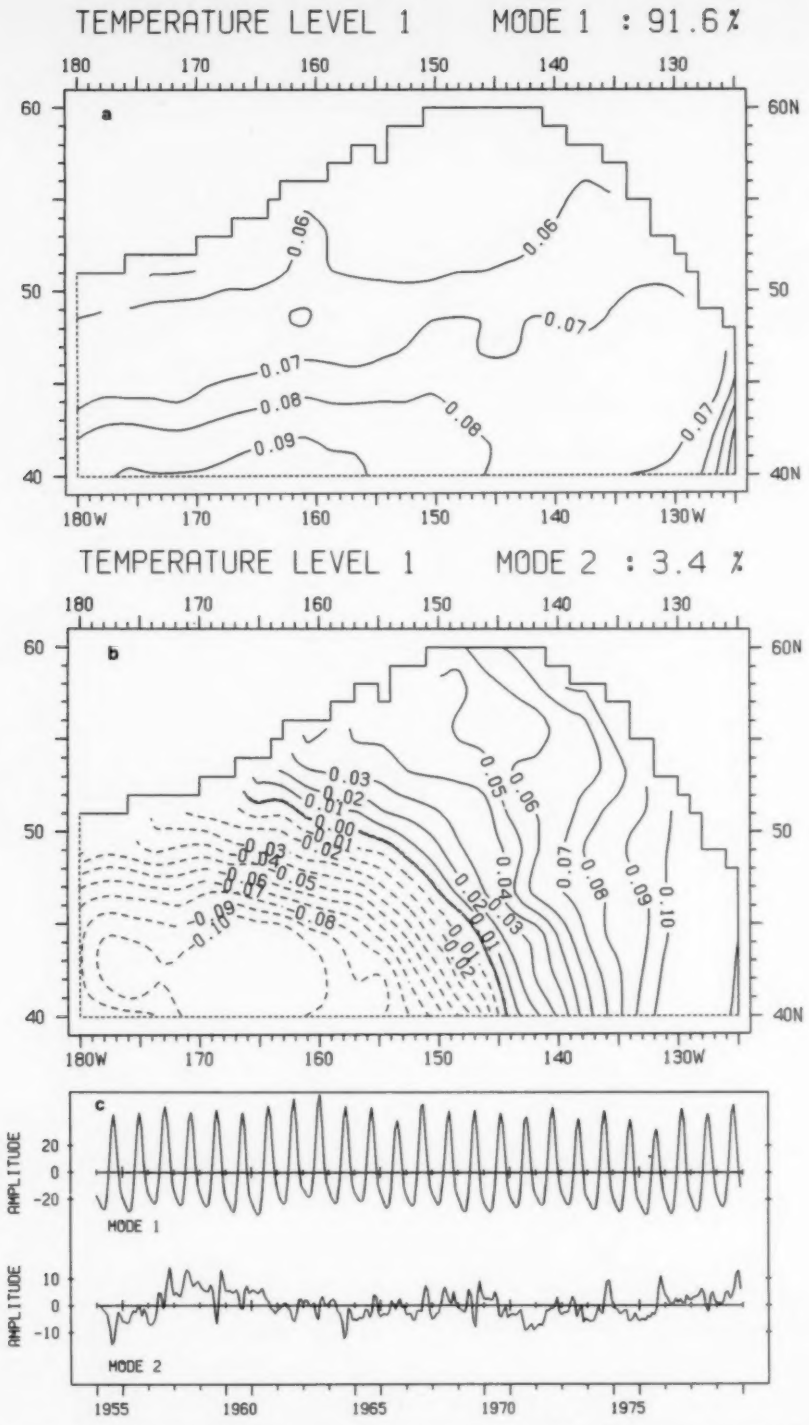

FIG. 3. Empirical orthogonal function modes $e_n(\underline{x})$ for the model surface temperature (at the 10-m depth level) for (a) mode 1, accounting for 91.6% of the total variance, and for (b) mode 2, accounting for 3.4% of the variance. Positive values are contoured by solid curves, negative values by broken curves. The patterns in Fig. 3a and 3b indicate that the temperature changes for mode 1 occur in unison over the whole domain whereas for mode 2, the temperature in the eastern half oscillates in opposition to that in the western half of the domain. (c) The amplitude $a_n(t)$ time series for these two modes reveal (*continued next page*)

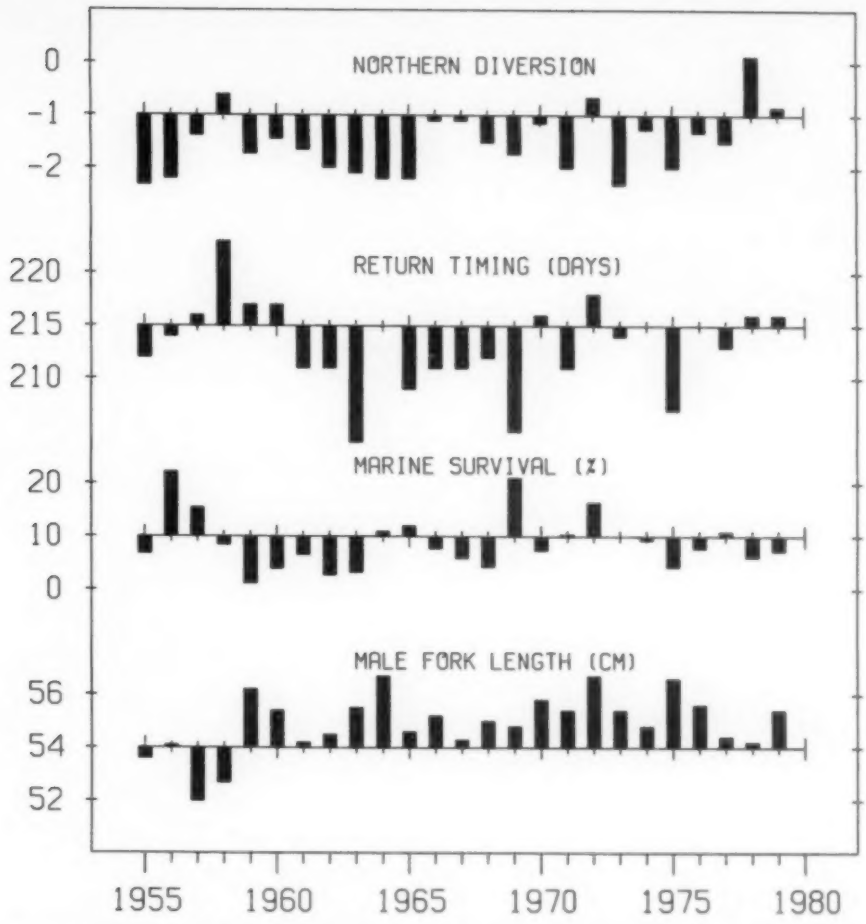

FIG. 4. Fraser River sockeye salmon annual time series. The northern diversion (% of sockeye returning via the northern route) scaled by the logit transformation (Xie and Hsieh 1989) (with low values denoting low diversion), followed by three Chilko River sockeye time series: return timing (in days from 1 January), marine survival (% adults/juveniles), and age 4_2 male fork length (cm).

as rather noisy, the number of "significant" cases for these "noisy" modes averaged to 2.9 cases (per mode per physical variable, Table 1), which provided a rough estimate of the number of "significant" cases arising by chance. Mode 2 averaged 7 "significant" cases in Table 1, which was more than twice the average for modes 3 and 4.

Conversely, we looked at the number of "significant" cases between an individual sockeye variable and the physical variables. The marine survival and fork length had the largest number of "significant" cases (Table 2), followed by the return timing and, much further behind, the diversion. This suggested that open ocean variability had the largest influence on the survival and size of returning adults and the least influence on the diversion of the return migration path.

To explore this further, we plotted the number of "significant" cases as a function of the time lags when significant correlation was found between the fish variable and the physical variable in the regression formula (2) (Fig. 5). This procedure may reveal the period in the fish life cycle when a particular physical variable has a strong influence on the fish. Return timing and fork length have their "significant" cases distributed mainly in two piles: early in the sockeye marine life and in the last 10 mo of their lives. This meant that return time and fork length were correlated with physical variables during the early marine life and towards the end of the marine life of the sockeye. Marine survival, while correlated with physical variables in the final 10 mos, showed few "significant" correlations with physical variables in the early marine life, somewhat contrary

FIG. 3. (*concluded*)
a strong annual cycle in a_1 and interannual variability in a_2. For instance, sharp rises in a_2 are found in the El Niño warming episodes of 1957–58, 1969, 1972, and 1976, which together with $e_2(\underline{x})$ implies that the eastern half of the Gulf of Alaska was warm, while the western half was cool during these episodes.

TABLE 1. Number of "significant" regression cases between the particular a_n representing a physical variable and a sockeye variable (with a total of 12 cases attempted for each a_n). The physical variables are surface air temperature (T_a), model surface temperature (T), windstress ($\underline{\tau}$), and model surface current ($\underline{u}$), with their first four modes ($n = 1,..,4$) used. The maximum correlation squared (r^2) between any individual term on the right-hand side of Eq. (2) and a sockeye variable is also given. The particular sockeye variable for which this maximum r^2 occurs is given in parentheses (d, diversion; t, return timing; s, marine survival; and l, fork length).

Variable	Mode	"Significant" cases	Max. r^2
T_a	1	0	
	2	9	0.30 (s)
	3	3	0.22 (l)
	4	2	0.21 (t)
T	1	1	0.18 (d)
	2	5	0.24 (s)
	3	0	
	4	5	0.26 (d)
$\underline{\tau}$	1	2	0.31 (t)
	2	7	0.47 (s)
	3	1	0.22 (l)
	4	6	0.42 (s)
$\underline{u}$	1	4	0.29 (t)
	2	7	0.32 (t)
	3	2	0.26 (t)
	4	4	0.27 (t)

TABLE 2. Number of "significant" regression cases between a sockeye variable and the physical variables (a_n for T_a, T, $\underline{\tau}$, and $\underline{u}$). The total number of regression cases tried for each sockeye variable was 48. The physical variable giving rise to the largest correlation squared (r^2) is given in parentheses.

Sockeye variable	"Significant" cases	Max. r^2
Diversion	7	0.27 ($\underline{u}$)
Return timing	14	0.32 ($\underline{u}$)
Marine survival	18	0.47 ($\underline{\tau}$)
Male fork length	19	0.30 ($\underline{\tau}$)

to our expectations. Northern diversion generally had few correlations with physical variables throughout.

We next examined the "significant" cases individually. We knew that the second modes for the air temperature and for the model surface temperature were closely related to El Niño episodes (Fig. 3b and 3c). The air temperature mode 2 in May–July of the sockeye return year was found to correlate significantly ($r = +0.48$) with the northern diversion, which indicated that El Niño warmings coincided with higher diversions, as expected.

Both air temperature and model surface temperature second modes in the summer months of the return year were significantly correlated with the Chilko River return timing (both around $r = +0.44$), with warm water in the eastern half of the Gulf of Alaska (Fig. 3b and 3c) coinciding with later return timing. Our result is reasonably compatible with the finding of Blackbourn (1987), where the Chilko return timing was found to be positively correlated with the average January–March SST during the return year in a 5 degree square area located in the eastern central Gulf of Alaska.

The surface temperature mode 2 in February–April of the return year was significantly correlated with marine survival ($r = -0.49$), as was the air temperature mode 2 in December–February ($r = -0.52$). Also, the surface temperature mode 2 in May–July of the sockeye's first year at sea was significantly correlated with marine survival ($r = -0.54$). All these correlations related higher temperatures in the eastern half of the gulf to lower marine survival rates.

Significant correlations between temperature and fork length were again revealed at two distinct times in the sockeye life cycle. Fork length was correlated with air temperature mode 2 in April–June of the first marine year ($r = +0.49$) and in May–July of the return year ($r = -0.50$). Fork length was also correlated with model surface temperature mode 2 in May–July of the first marine year ($r = +0.40$) and in May–July of the return year ($r = -0.44$). The signs of the correlations indicated that warmer temperatures in the eastern half of the Gulf of Alaska early in the sockeye marine life were correlated with greater fork length (in the returned mature sockeye), but warmer temperatures during the return migration were correlated with shorter fork length.

Let us examine the vector EOF's. As mentioned earlier, with vectors such as windstress and current, the temporal amplitude a_n is complex, with a component governing the length (or strength) of the vectors in the EOF and the other the rotation of the entire EOF pattern. These components will be referred to as the first and the second components. For instance if a current pattern increases in strength, then the first component of a_n increases, while if the pattern merely rotates to a different orientation, only the second component changes. With windstress, the first component of a_n of both modes 1 and 2 in the fall of the first marine year was significantly correlated with the return timing ($r = -0.56$ and $r = -0.55$, respectively). With currents, the first component of a_n for mode 2 in March–May in the return year was correlated with the fork length ($r = 0.48$). The orientation of the currents may have influenced the diversion, as the second component of a_n for mode 1 in May–July and for mode 2 in January–March of the return year was correlated with the diversion ($r = -0.52$ and $r = 0.47$, respectively).

Discussion and Summary

In this paper, a novel approach to fishery management is initiated which, when fully developed, is analogous to using numerical weather prediction to plan agricultural activities. The success of this approach hinges on two conditions: (1) Can accurate numerical ocean prediction be developed? and (2) If scientists have access to accurate numerical ocean prediction, is their knowledge of the response of marine organisms to changing environmental conditions enough to allow them to utilize the forecasts?

With our present state of knowledge, neither condition is satisfied. Despite considerable computation cost, our numerical model of the northeast Pacific Ocean remains inadequate due to the lack of accurate surface forcing data (surface freshwater flux and heat flux), coarse grid resolution, coarse bottom topography (W. G. Lee, G. Holloway, and W. W. Hsieh, unpubl. data), and the presence of unrealistic side boundaries. Furthermore, the monthly atmospheric forcing data do not resolve the individual weather systems and are only available many years later.

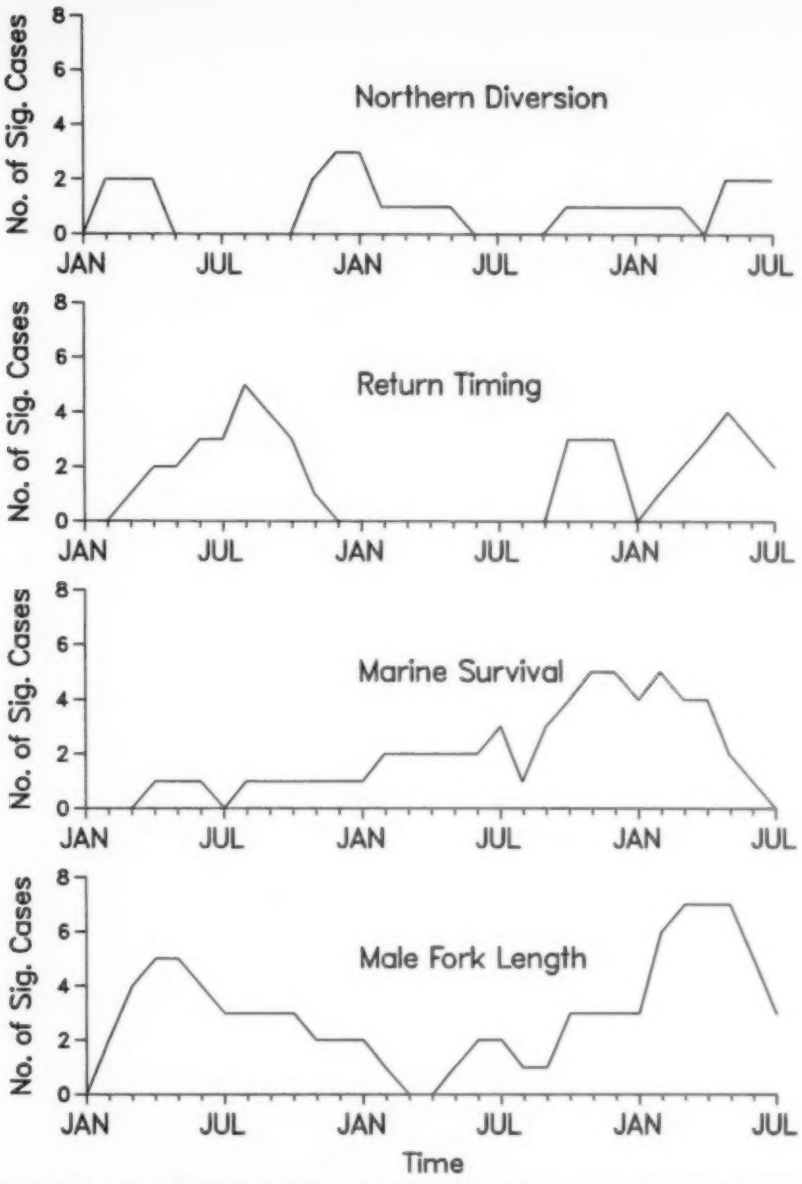

FIG. 5. Number of "significant" regression cases between a sockeye time series and physical variables at various time lags to the past. A large number of "significant" cases at a particular time would indicate that at this period in the sockeye's life cycle, one or more physical variables appear to exert an influence on the sockeye. The time scale has January in the year of the juvenile's entry into the ocean on the far left and July in the year of the sockeye's return on the far right. Fraser River sockeye normally spend three summers and two winters in the open ocean.

The second problem of connecting the massive amount of model output to fish variables is equally difficult. First, the output has to be dramatically condensed. While EOF analysis is useful in condensing the data over the entire model domain, it is useless if a fish variable depends on a very local environmental change, which would account for only a small fraction of the total variance over the model domain, and hence would not manifest as an important mode under the EOF analysis. Our "shotgun" approach to finding relations between the physical variables and the fish variables does not completely screen out spurious correlations. Clearly, one needs to investigate further what statistical techniques can best link the huge amount of model output to fish variables.

How important is the ocean model? If we regress the atmospheric data with the fish variables directly, how do the results compare with using the atmospheric data to drive an ocean model and then regressing the model output with the fish variables? The number of "significant" regression cases with fish

variables for air temperature T_a and model surface temperature T is 14 and 11, respectively, and for windstress and surface current is 16 and 17, respectively (Table 1). Hence, we cannot conclude that there is significant advantage in using the model ocean variables over the atmospheric data. However, this behaviour could have resulted from our use of EOF's, which detected the large-scale features in the atmosphere and the ocean, which could be strongly coupled. (For instance, T_a and surface T are rather similar, although the windstress and surface currents are not.) If fish variables were related to local ocean features (e.g. currents in a particular region), then the value of an ocean model would be increased. As we did not try relating fish variables to local ocean variables, our evaluation of the advantage of using an ocean model over atmospheric data did not give full justice to the ocean model.

In summary, we have made what we believe is a novel and original attempt on a very difficult problem. Despite a limited numerical model, we have some evidence that the EOF modes associated with interannual variability (usually mode 2) were more often correlated with the fish variables than the other modes thought to contain mainly the seasonal cycle or noise. Our regression study confirmed two known results: higher temperature in the eastern half of the Gulf of Alaska during the return year was correlated with (1) higher northern diversion and (2) later Chilko River return timing. In addition, we found that higher temperature was correlated with lower marine survival. Higher temperature early in the sockeye marine life was correlated with greater fork length when the mature fish returned, but higher temperature during the return year was correlated with shorter fork length. Windstress in the first marine year was correlated with the return timing, while currents in the return year were correlated with the fork length and the diversion. The correlations between the physical variables and the sockeye variables suggested that the physical variables exerted most influence in the first and final few months of the sockeye marine life.

Using atmospheric data and a limited ocean model, we have found links between the large-scale atmosphere–ocean variability and variability in the sockeye salmon. In the near future, increasingly accurate ocean models and improved data techniques will enhance the significance of these links. The coupling of ecosystem models (with nutrients and plankton, etc.) to the ocean general circulation model will fill the present gap between the physical variables and the fish variables, thereby further confirming any discovered links between oceanic variability and fish variability.

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Temporal Variability in Antarctic Marine Ecosystems: Periodic Fluctuations in the Phocid Seals

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Three species of seals around Antarctica have shown quasi-cyclic patterns in some aspect of their biology: the age structure of crabeater seals (*Lobodon carcinophagus*) around the Antarctic Peninsula has shown strong cohorts separated by 4- to 5-yr intervals; juvenile leopard seals (*Hydrurga leptonyx*) have appeared in unusually large numbers at Macquarie Island, also at 4- to 5-yr intervals; and Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound have undergone fluctuations in reproductive rate every 4–6 yr. Complex demodulation was used to compare patterns among these three data sets and with the Southern Oscillation Index (SOI). All of the seal data sets showed evidence of cyclical behavior when demodulated at a period of 5 yr. The Weddell seals were generally in phase with the SOI since the Weddell series began in 1970. The leopard seals and SOI were in phase in the 1960's, but thereafter the SOI series led the leopard seal series by about one quarter of a cycle. The crabeater series was more complicated, but similarities with the other data sets also were seen. If these tentative observations are confirmed, they point to large-scale oceanographic variation, possibly related to the El Niño – Southern Oscillation (ENSO), as an important mechanism in Antarctic marine ecosystems.

Trois espèces de phoques qui vivent en bordure de l'Antarctique manifestent un comportement quasi-cyclique dans un certain aspect de leur biologie : on observe dans la structure par âge du phoque crabier (*Lobodon carcinophagus*) qui vit autour de la Péninsule antarctique des cohortes importantes séparées par un intervalle de 4 ou 5 ans; des phoques-léopards juvéniles (*Hydrurga leptonyx*) sont apparus en remarquable abondance à l'île Macquarie, également à intervalles de 4 ou 5 ans; enfin, des populations de phoques de Weddell (*Leptonychotes weddellii*) du détroit de McMurdo ont subi des fluctuations de leur taux de reproduction tous les 4 à 6 ans. Une démodulation complexe a servi à comparer entre elles les variations cycliques de ces trois ensembles de données ainsi qu'à les comparer à l'indice de l'Oscillation australe (IOA). Les trois ensembles de données sur les phoques présentaient des signes d'une variation cyclique lors d'une démodulation selon une période de cinq ans. Depuis son commencement en 1970, la série des phoques de Weddell était généralement en phase avec celle de l'IOA. Celle des phoques-léopards et celle de l'IOA étaient en phase au cours des années soixante, mais par la suite, celle de l'IOA a devancé la série des phoques-léopards d'environ un quart de cycle. La série des phoques crabiers était plus complexe, mais des similitudes avec les autres ensembles de données étaient également reconnaissables. Si elles sont confirmées, on pourra conclure que ces observations pointent vers une variation océanographique à grande échelle, peut-être en relation avec l'El Niño – Oscillation australe (ENSO), qui constituerait un mécanisme important dans les écosystèmes marins de l'Antarctique.

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In the Antarctic, as elsewhere, pinnipeds are at or near the top of the trophic pyramid (Laws 1977, 1984) and thus their behavior, as a response to environmental features, integrates perturbations lower in the food web. Variations in certain biological features of top-level predators have recently drawn attention to their potential as indicators of underlying ecological or oceanographic perturbations (e.g. Schreiber and Schreiber 1984; Croxall et al. 1988). We focus here on data from three species of phocid seals that have shown quasi-cyclic patterns in some aspect of their biology: the age structure of crabeater seals (*Lobodon carcinophagus*) around the Antarctic Peninsula (Fig. 1) has shown strong cohorts separated by intervals of 4–5 yr (Laws 1984; Bengtson and Laws 1985); juvenile leopard seals (*Hydrurga leptonyx*) have appeared in unusually large numbers at Macquarie Island (Fig. 1), also at intervals of roughly 4–5 yr (Rounsevell and Eberhard 1980; Rounsevell 1988); and Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound (Fig. 1) have undergone fluctuations in reproductive rate every 4–6 yr (Testa 1987). A comparison of three Weddell seal populations around Antarctica also suggests that roughly synchronous reproductive fluctuations are occurring at nearly opposite sides of the continent (Testa et al. 1990). Because these observations span a large part of the Southern Ocean, their similarity suggests that a large-scale oceanographic mechanism must be invoked to explain biological events having such a similar period. One such phenomenon, the El Niño – Southern Oscillation (ENSO), is widely acknowledged to display similar periodicity (Graham and White 1988; Enfield 1989) but is not usually thought to influence weather or ocean patterns around Antarctica. However, atmospheric anomalies associated with ENSO do occur in the Southern Ocean (van Loon and Shea 1987; Priddle et al. 1988). The widespread occurrence of these quasi-cyclic seal phenomena and similarity in period to a well-known and nearly global climatic event prompted us to reexamine the seal data for explicit evidence of their periodicity, the temporal relationships among them, and possible correspondence to ENSO.

Methods

Data from a tagged population of Weddell seals were used to estimate yearly adult reproductive rates in McMurdo Sound (166°45′E, 77°45′S) (Fig. 1) from 1970 to 1987 (Testa 1987; Testa and Siniff 1987; Testa et al. 1990). Reproductive rate was defined as the proportion of adult females over 7 yr old that were seen with a pup in each spring (November).

The number of leopard seals that hauled out on beaches was counted annually at Macquarie Island (159°00′E, 54°30′S) from 1949 to 1986, excepting 1950 and 1958 (Rounsevell and Eberhard 1980; Rounsevell 1988). We used the continuous data (transformed by $\log_{10}$) from 1959 to 1986 in the analysis.

Age structure in crabeater seals was estimated from seals collected in the vicinity of the Antarctic Peninsula (58–64°W) since 1964; seals were aged by counting cementum annuli in the teeth (Laws 1953). The sample comprises 2122 seals collected from 1964 to 1986 (Øritsland 1970; Laws 1984; Bengtson and Laws 1985; Lowry et al. 1988; J. L. Bengtson, unpubl. data). The year of collection was standardized as the year of the nearest spring (October), when pups are born. We estimated the strength of each crabeater seal cohort, correcting for age structure and sample size using a generalized linear model. This model and its derivation are discussed in detail in the Appendix.

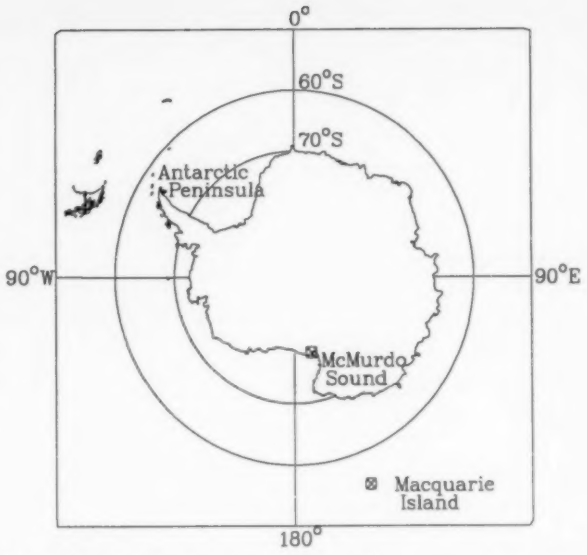

FIG. 1. Map of Antarctica showing the locations of research sites providing seal data.

The most widely used Southern Oscillation Index (SOI) is the standardized Tahiti minus Darwin sea level pressure anomaly (Trenberth 1984). We used a 5-mo running average of these values from 1944 to 1987 (U.S. Department of Commerce 1959; Trenberth 1984; van Loon and Shea 1987).

All of the data sets show evidence of cyclical behavior (Rasmussen and Carpenter 1982; Laws 1984; Testa 1987; Rounsevell 1988). One way to examine cyclic data is via complex demodulation (Bloomfield 1976), which models the data as a cosine curve with a fixed period (p), slowly varying the amplitude (R_t) and phase (ϕ_t):

$$y_t = R_t \cos\left(\frac{2\pi}{p}t + \phi_t\right)$$

and then estimates the amplitude and phase via a smoothing operation. (The phase, ϕ_t, is measured in radians. It is sometimes helpful to use an alternative phase measured in years: $\phi'_t = p\,\phi/2\pi$. Later references to phase in years will be to the phase ϕ'_t.) Complex demodulation is analogous to fitting a cosine curve with a fixed period to a narrow, sliding window of the data and permits determination of the timing of peaks, true local period, and so forth.

We standardized all seal data sets by dividing by their standard deviations prior to complex demodulation. A pure cosine curve has variance 0.5, so that a cosine curve standardized to unit variance has amplitude $\sqrt{2}$. Thus, the estimated amplitude divided by $\sqrt{2}$ is analogous to a correlation coefficient in regression. Stretches of the data with strong, well-defined cycles will have large estimated amplitude; stretches of the data with small estimated amplitude either have little power at that period or have a sharp change of phase. A slight upward trend in the estimated phase indicates that the true local period is shorter than the demodulation period, while a slight downward trend implies that the true local period is longer. If s is the slope of the estimated phase, then the true local period is about $2\pi p/(2\pi + sp)$.

We demodulated the three seal data sets and the SOI at the period of 5 yr using a smoothing window of 5 yr. (The width of the smoothing window controls the degree to which the phase is local. A wider window would smooth much of the roughness, but would also lose the finer structure.) We examined the synchrony of the data series by looking at phase difference plots showing the time series $\sqrt{R_{1t}R_{2t}}\exp(i(\phi_{1t}-\phi_{2t}))$. Points plotted along the positive real axis are in phase; points plotted along the positive imaginary axis occur when series 1 is one quarter of a cycle ahead of series 2 and so on. Distance from the origin reflects the strength of the cycles on a scale of 0 to $\sqrt{2}$.

Our analyses were suggested by the data and valid statistical tests are therefore not possible. The results serve more to suggest patterns and relationships that should be tested when additional data are available.

Results

Figure 2 shows the time series of the three seal data sets and the SOI. Figure 3 shows the four time series of estimated phase. The Weddell seal data showed a nearly constant phase and local period of 5 yr, except for a small phase shift in 1979 when the cycle was retarded about 0.8 yr (Fig. 3). Patterns in the leopard seal data are more complicated. From 1962 to 1970 the local period was stable at about 5.1 yr. Then in the early 1970's, a large phase shift corresponding to an advance of about 2.1 yr occurred in the cycle (both 1971 and 1973 were low years for the leopard seal counts). From 1973 to 1981 the period was about 5.9 yr. After 1981 the period reverted to 5 yr.

Visual inspection of the crabeater data (Fig. 2) showed an interesting pattern: a long cycle, a short cycle, a long cycle, a short cycle, three roughly 5-yr cycles, and finally a long cycle. Complex demodulation interprets the long/short pattern as long cycles with phase shifts. Until 1962 the period was about7.5 yr, but there was a phase shift in 1952 corresponding to an advance of 3.4 yr. From 1962 to 1975 the cycle was stable at 5 yr, but lengthened to 8 yr after 1976.

Weddell seals generally led the leopard seals by about one quarter of a cycle (Fig. 4a), although they were nearly out of phase in the late 1970's and nearly in phase by the mid-1980's. Weddell seals led crabeater seals by one quarter to three eighths of a cycle (Fig. 4b). Correspondence between the leopard and crabeater seal data was much weaker. During the 1960's the crabeater series led leopard seals by about one quarter of a cycle; in the 1970's the two series were roughly in phase; in the early 1980's the leopard seals began to lead the crabeater seals; and by 1983 the series were essentially out of phase (a peak in the crabeater seal data matching a trough in the leopard seal data).

We repeated the analysis of phase differences by examining the seal series and the SOI (Fig. 5). The Weddell seals were generally in phase with the SOI, with troughs matching troughs since the Weddell series began in 1970. The leopard seals and SOI were in phase in the mid-1960's, but thereafter the SOI series lead the leopard seal series by about one quarter of a cycle. The crabeater series is more complicated. In the 1950's the SOI led the seals by about three eights of a cycle; in the 1960's the seals led the SOI by one eighth to one quarter of a cycle; in the 1970's and 1980's, the SOI again led the seals by one quarter to one half of a cycle.

Discussion

The seal data series are widely separated geographically, represent three ecologically diverse species of seals, and reflect events of different biological significance. It may help to characterize fluctuations in the three series in a biological context.

Weddell seals are mostly neritic, frequenting the nearshore areas of Antarctica where annual sea ice is attached to shore and provides almost complete surface cover (Stirling 1969). Weddell seals in McMurdo Sound during summer feed primarily on a small, midwater fish species, *Pleuragramma antarcticum*, although other fish, cephalopods, and crustaceans are also eaten (Testa et al. 1985). Although juveniles disperse, adults probably remain within tens of kilometres of traditional breeding colonies (Stirling 1974; Testa and Siniff 1987). The reproductive changes observed in the McMurdo Sound population are not apparently related to annual variation in the extent of shorefast ice in spring, or to seal population size (Testa and Siniff 1987). Declines in reproductive rate are most likely to be energetically mediated as a result of decreased food availability during gestation over winter. Possible causes for interannual changes in food availability include variation in the overwinter availability of shorefast sea ice for Weddell seals, large-scale fluctuations in *P. antarcticum* population size (assuming its importance in the diet during winter), or changes in the ocean circulation that transports pelagic fish into seal-inhabited areas (Testa and Siniff 1987; Testa 1987).

In contrast with Weddell seals, both crabeater and leopard seals are pelagic and reside in the continually shifting pack ice surrounding Antarctica. The geographic extent of their movements is undoubtedly large, compared with Weddell seals. Leopard seals near the Antarctic Peninsula feed mostly on Antarctic krill (*Euphausia superba*), but fish, penguins, and crabeater seal pups are also taken during the spring and summer (Siniff and Stone 1985; Lowry et al. 1988). Macquarie Island lies well to the north of the usual extent of pack ice, and the occurrence of leopard seals there reflects a northward dispersal during winter. The age structure of Macquarie sightings in a short sequence of years was skewed toward young seals, especially yearlings, and did not indicate that a peak of leopard seal counts was caused by a single strong cohort (Rounsevell and Eberhard 1980). Rather, peaks in the number of leopard seals at Macquarie represent juvenile dispersal in response to conditions in the pack ice to the south. The dominance of krill in the winter diet of leopard seals (Siniff and Stone 1985) suggests a link to krill abundance or availability.

Of the three species, crabeater seals are the most specific in their diet, feeding almost exclusively on krill near the Antarctic Peninsula (Øritsland 1977; Lowry et al. 1988), although more opportunistic feeding has been noted elsewhere in Antarctica (Green and Williams 1986). Variations in crabeater seal age structure can arise from fluctuations in productivity, or later interactions of particular cohorts with age-specific survival factors, especially juvenile survival (Testa 1990). Again, prey availability is a likely determinant of whether a year is favorable or unfavorable, but that availability could result from changes in the standing stock of krill or the distribution and extent of pack ice (and hence, seals) in the region. Another possible determinant of crabeater cohort strength is predation impact of leopard seals on crabeater seal pups in their first summer, when pups are most vulnerable. Of the three data series from Antarctic seals, the crabeater age structure is the furthest removed in time from causal events in the environment, and patterns in environmental fluctuations, if they exist, are likely to be dampened or displaced in the age structure (Testa 1990).

The possibly cyclic nature of the fluctuations is one of the most interesting aspects of these data. The Weddell seal series

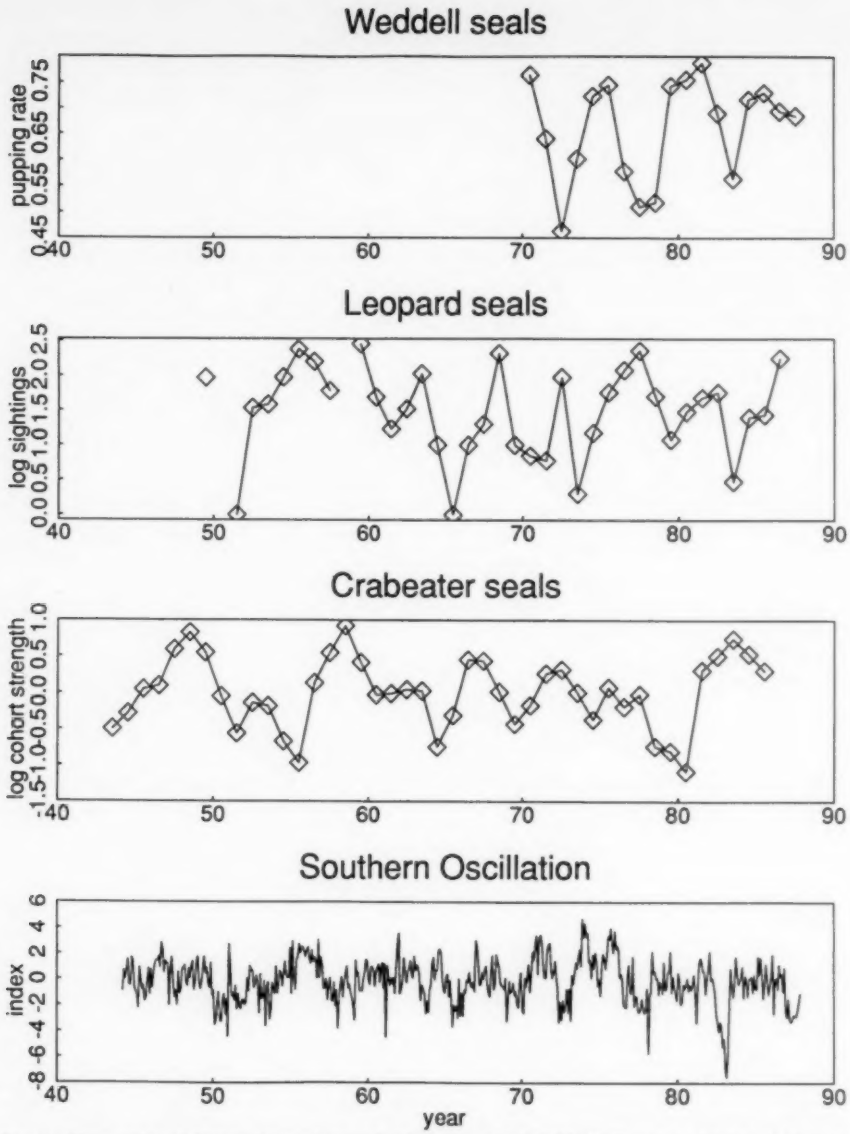

FIG. 2. Time series of (top to bottom) reproductive rates of adult Weddell seals in McMurdo Sound, $\log_{10}$ numbers of leopard seals seen annually on Macquarie Island, and relative strengths of crabeater seal cohorts estimated from collections made in the vicinity of the Antarctic Peninsula (see text).

provides the clearest illustration of this, with a cycle that is nearly pure (Fig. 3), and a strong relationship to both the leopard seal and the SOI data series (Fig. 4a and 5a). It is, however, the shortest series considered here. Our prediction, based on continuation of the strong cycle shown thus far, was that a reproductive decline among McMurdo Weddell seals was due in 1988. Instead, a small decline was seen in 1986, matching a trough in the SOI, and a stronger decline was seen in 1989, again matching a mild trough in the SOI (J. W. Testa, unpubl. data). The purity of the 5-yr cycle is therefore likely to have changed, while the relationship with the SOI has continued.

In view of the different ecological roles played by leopard and Weddell seals, the apparent correspondence between these two data series is somewhat surprising and suggests common cause, direct or indirect. The significant events, troughs in Weddell seal reproduction and peaks in leopard seal dispersal, are both most likely to arise from poor conditions for the respective populations, and both occur at roughly the same time (Fig. 2) in areas separated by about 7° of longitude and perhaps 15° of latitude (based on the average northward extent of pack ice in winter). There are few data on physical parameters in the area: neither temperature nor large-scale extent of sea ice in the region from 1973 to 1981 (Zwally et al. 1983) was correlated with the Weddell or leopard seal data. Temperature data directly from McMurdo Sound (Jacobs and Comiso 1989) also showed no correspondence with the Weddell seal data.

The crabeater seal data were collected on the opposite side of Antarctica from the other seal study sites, and farthest from the locations of the atmospheric pressure conditions used in the SOI. The consistency of cyclic features in the crabeater data,

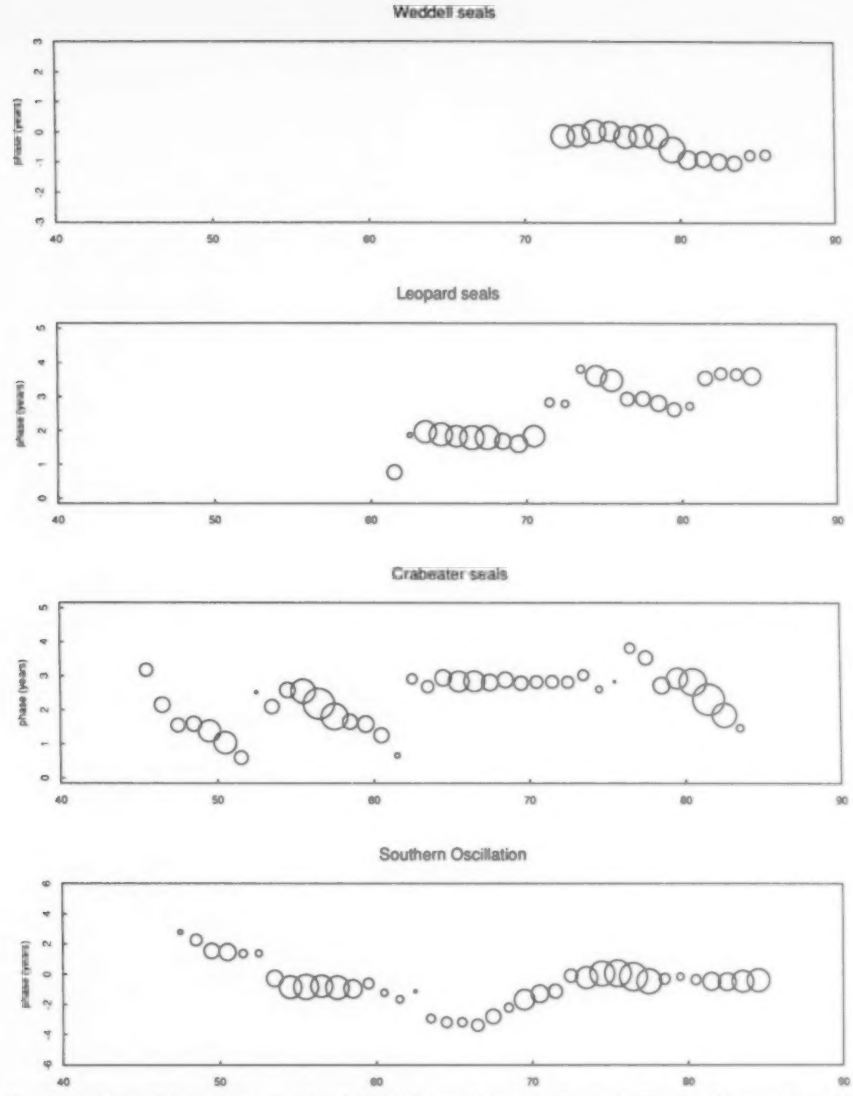

FIG. 3. Estimated phase from complex demodulation of the data shown in Fig. 2 using a period of 5 yr and a smoothing window of 5 yr. The radii of the plotted circles give the amplitude in x-axis units. The maximum possible radius is $\sqrt{2}$.

and their similarity and synchrony with the other data sets is, not surprisingly, more tenuous. Cohort strength measured retroactively is a much more complex parameter than reproductive success or juvenile dispersal. The statistical analysis used on the crabeater collections assumed a constant age-specific survival schedule, and our model assigned the cyclical variation to relative cohort strengths. Juvenile survival in large mammals can vary substantially (Fowler 1987), and the peaks (or troughs) in cohort strength can be offset from peaks (or troughs) in environmental carrying capacity by 0–2 yr, depending on the variability of juvenile survival relative to that of adult reproductive rates (Testa 1990). Also, age determination from tooth anulli, particularly for older seals, includes errors. Such effects could add "noise" to any signal in crabeater age structure being generated by large-scale ecological or climatic events. However, it is interesting that the most dramatic phase shifts in the crabeater and SOI series occurred at the same time (Fig. 3). Also, indices of Weddell seal reproductive rates from McMurdo Sound and Signy Island (northeast of the area from which crabeater seals were collected) were roughly in phase (Testa et al. 1990). This suggests that the oceanographic or ecological events affecting seals in the two regions are not independent.

While the consequences of ENSO events are now known to be nearly global, little attention has been given to the relationship of the Southern Ocean to ENSO. van Loon and Shea (1987) showed that strong sea level pressure anomalies extend to several areas around the coast of Antarctica before and during the typical ENSO event. Priddle et al. (1988) found sea level pressure anomalies northeast of the Antarctic Peninsula that correlate well with ENSO variables, and they suggested that the resulting changes in wind stress caused disruption of the mesoscale oceanic gyres in that area and dispersal of normally high

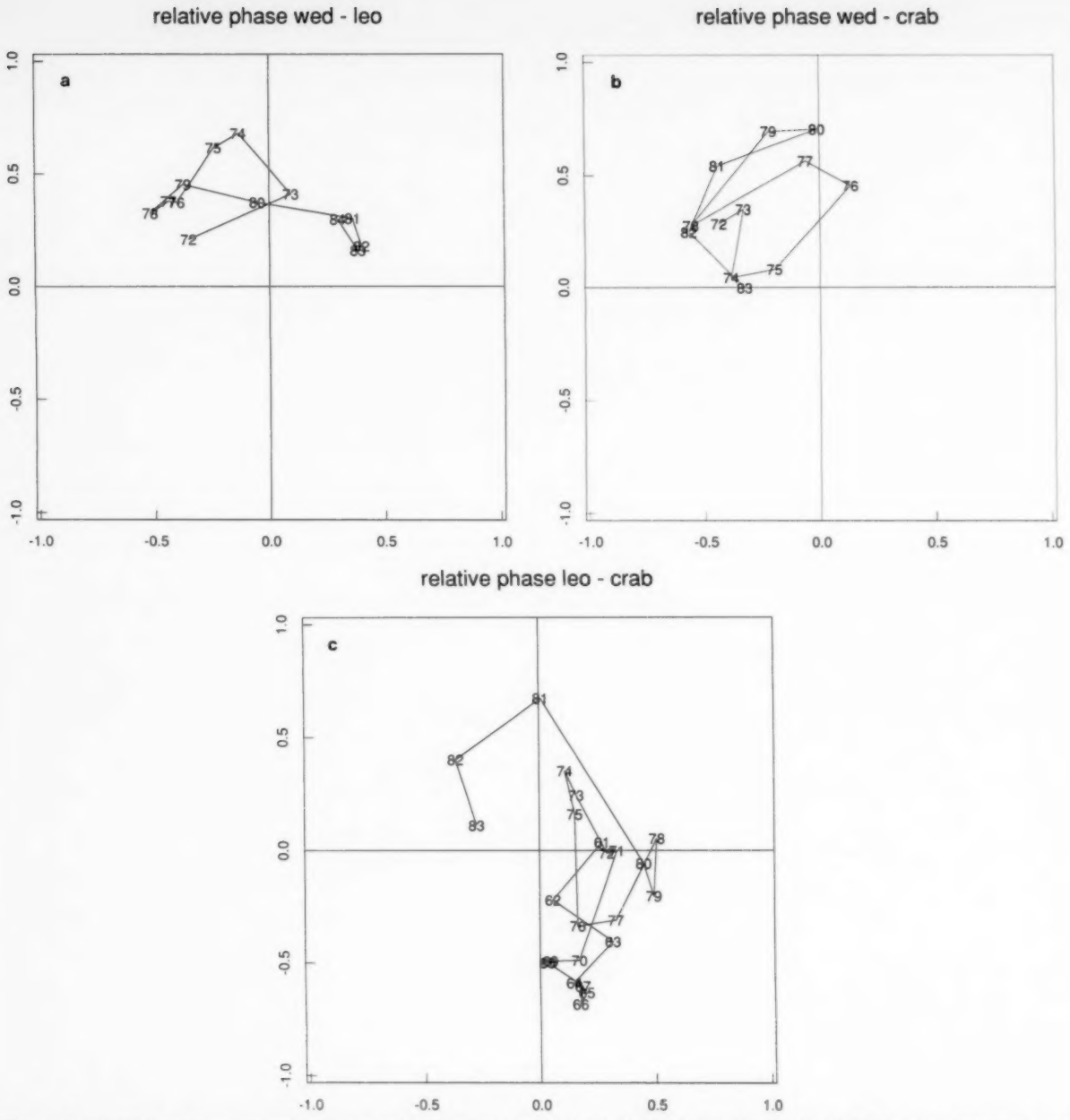

FIG. 4. Phase difference plots comparing the time series demodulation of (a) Weddell and leopard seals, (b) Weddell and crabeater seals, and (c) leopard and crabeater seals. Points along the positive real (horizontal) axis are in phase; points denote increasing lag by species 2 as one goes counterclockwise on the chart. Distances from the origin reflect the strength of the cycle with a maximum possible value of $\sqrt{2}$.

krill concentrations. This would account for the poor reproductive success that was observed in krill-dependent vertebrates at South Georgia a year after El Niño (Croxall et al. 1988). A similar disruption of prey availability to Weddell seals in McMurdo Sound could occur as a result of anomalous wind stress and current patterns in the Ross Sea region. Overwinter current patterns in McMurdo Sound have recently been studied (Barry and Dayton 1988), but the long-term patterns are still unknown. We might expect that time lags and oceanographic/weather phenomena that have been observed to complicate ENSO effects in areas remote from the tropics in the Northern Hemisphere (Emery and Hamilton 1985; McLain et al. 1985; Ainley et al. 1988; Ainley and Boekelheide 1990) could operate in the Southern Ocean, although van Loon and Shea (1987) found teleconnections to be more direct in the Southern Hemisphere than in the north. Also, dissimilarities in period between SOI and the seal data (Fig. 3) may not rule out the influence of ENSO events in the Southern Ocean if the effects are intermittent or mediated through a long causal chain.

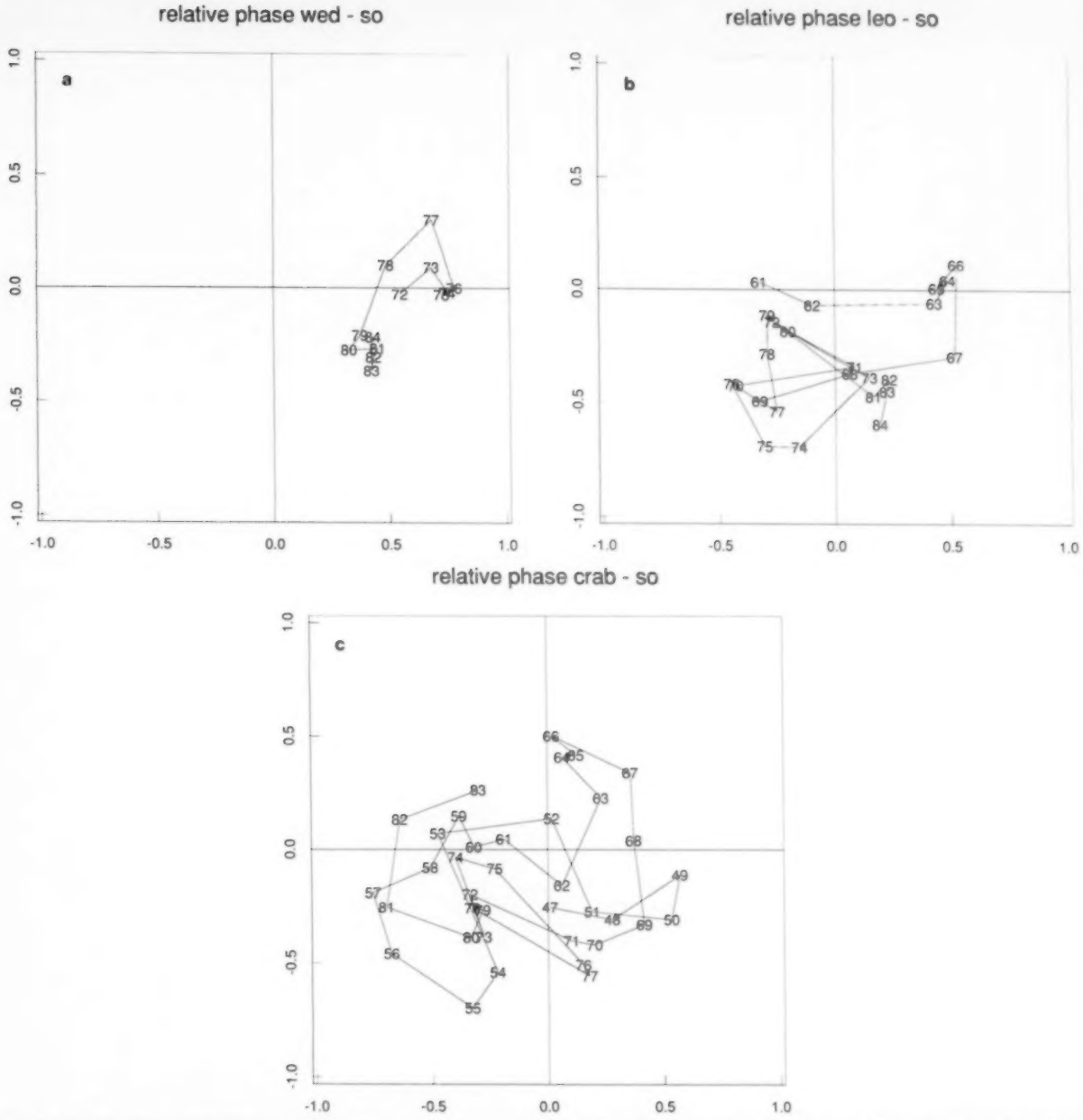

FIG. 5. Phase difference plots comparing the time series demodulation of (a) Weddell seals, (b) leopard seals, and (c) crabeater seals with the SOI. Points along the positive real (horizontal) axis are in phase; points denote increasing lag by the SOI as one goes counterclockwise around the chart. Distances from the origin reflect the strength of the cycles with a maximum possible value of $\sqrt{2}$.

The evidence presented here is suggestive of links between the data sets shown, but contradictions are apparent. Our intent is to provoke discussion and expanded research on the causes of variability in elements of Southern Ocean ecosystems, and the possibly cyclic nature of this variability. Similar patterns may exist in Arctic marine ecosystems. Further evidence of direct causal connections between these disparate elements of the Antarctic ecosystem and with long-term climatic patterns is needed. If climatic effects on seals are mediated through productivity in the food chain, or if the cyclic patterns seen in these data are part of an intrinsic cycle in the Antarctic marine ecosystem unrelated to climatic fluctuations, then the causal pathways may be difficult to delineate.

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Appendix: Estimation of Cohort Strengths of Crabeater Seals

Only the large collections (>300) of 1972, 1973, and 1981 allowed using seals up to 30 yr of age. All other collections were truncated at age 20. With these restrictions, the data took the form of collections in 15 of 22 years (n = 22–526). Variation in sample size was a function of sampling effort expended and seal distribution, not total seal population. We estimated the strength of each crabeater seal cohort, correcting for age structure and sample size. Let $p_{i,j}$ be the population of seals of age i in collection year j: these animals were born in year $j - i$. We assumed that the seals taken during a collection were captured at random with respect to age and that the total collection size N_j is fixed. This implies that the vector of sample sizes by age for collection year j, $Y_j = (Y_{1,j}, Y_{2,j}, \ldots, Y_{30,j})^T$ follows a multinomial probability distribution with parameters N_j and $p_{i,j}/\Sigma p_{i,j}$). We modelled $p_{i,j}$ as the product of cohort strength in cohort year $j - i$ and survivorship at age i, assuming a com-

mon survival function for all cohorts. We used Siler's (1979) log survival curve based on competing risks for animal mortality:

$$\ln s_i = -(a_1/b_1)(1-e^{-b_1 i}) - a_2 i + (a_3/b_3)(1-e^{b_3 i}).$$

The a and b parameters of this model are all positive and the three terms are interpreted as juvenile, mature, and senescent components of survival (s_i) to age i. A statistically equivalent and computationally more convenient form of the model is obtained as follows. Assume that each observation $Y_{i,j}$ follows a Poisson distribution with mean $u_{i,j}$:

$$\ln(u_{i,j}) = e_j + c_{j-i} + \ln s_i.$$

The c_{j-i} term is the log of cohort strength in cohort year $j - i$. We loosely interpret the e_j term as "effort" expended in the jth collection, but the e_j term is needed solely to make the Poisson and multinomial models equivalent, effectively by correcting for sample size.

It is well known that population size cannot be uniquely recovered from age structure data alone. For example, a population with constant-sized cohorts and an exponentially decreasing survival function can have the same age structure as a population that has no mortality and has exponentially increasing cohorts. This phenomenon is present in our model, as any change in ln cohort strength that is linear in time will be confounded with the linear term (mature hazard) of Siler's (1979) model. We assumed that all linear changes were due to survival effects and that none were due to a linear trend in cohort year effects. This is most easily accomplished by fitting the model without the mature hazard term, and then removing any linear trend from the cohort year affects c_{j-i}. The slope in c_{j-i} is our estimate of a_2.

The assignment of the linear portion to age structure is arbitrary, but in the absence of additional data on population size, some such assumption must be made to uniquely estimate the parameters. In any event, we are interested in short-term cyclical patterns in the cohort strength, and the slight linear trend of ambiguous origin effects these cycles only slightly.

For fixed b_1 and b_3, this survivorship model is a generalized linear model in the sense of McCullagh and Nelder (1983) and can be fitted using the GLIM statistical software package (Baker and Nelder 1978). This software provides maximum likelihood estimates of the parameters e_j, a_k, and c_{j-i} plus standard errors and other inferential quantities. To get maximum likelihood estimates of the b_k parameters, a grid search over the possible values of the b_k was performed minimizing the deviance of the GLIM fit. (The deviance is the generalized linear model analogue of the error sum of squares in regression.) An equally good fit for log survival, although of less biological significance, could be obtained using a polynomial of age, instead of Siler's (1979) hazards model.

The data were overdispersed; that is, they showed greater than multinomial (or Poisson) variation. The source of this overdispersion is not known, although there are several possible mechanisms. For example, if seals were sampled in a multinomial fashion from herds with age structures that varied about the population age structure, then the sampled population age structure will show greater than multinomial variability. Two methods were examined to correct for this overdispersion. First, we tried including additional explanatory terms, such as separate juvenile or senescent hazards for each cohort year. While these terms were significant, the overall fit of the model remained poor. Second, we examined the negative binomial and variance proportional to mean, quasi-likelihood models (McCullagh and Nelder 1983, chap. 6 and 8). The variance proportional to mean model has the same estimates as the Poisson model, but the variances are scaled upward to reflect the overdispersion. The negative binomial model differs from the rescaled Poisson mostly in that counts with large expectation (say greater than 10) have a larger variance under the negative binomial model. The two models are quite similar for counts with small expectation. Both overdispersed models fit the data adequately, and examination of residuals did not indicate systematic differences based on model. Since the overdispersed Poisson model (variance proportional to mean) is easiest to understand and implement, and produces results very similar to the negative binomial, we elected to use it for the remainder of the analysis. Examination of the residuals, however, revealed that pup counts fit all models poorly. Because pups may be collected differently and fit our models so poorly, we decided to use estimates of cohort strength based on counts excluding pups. The GLIM analysis of crabeater seal age structure resulted in the following hazard parameters (Siler 1979): $a_{1-3} = 0.74$, 0.32, 0.020; $b_1 = 0.62$; and $b_3 = 0.14$.

Evaluation of Methods for Separation of Gulf of St. Lawrence Beaked Redfishes, *Sebastes fasciatus* and *S. mentella*: Malate Dehydrogenase Mobility Patterns Compared with Extrinsic Gasbladder Muscle Passages and Anal Fin Ray Counts

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Malate dehydrogenase (MDH) electrophoretic mobility patterns were used as a standard against which field methods involving anal fin ray counts (AFCs) and extrinsic gasbladder muscle (EGM) rib passage patterns were compared to separate the beaked redfish species, *Sebastes fasciatus* and *S. mentella*. The frequencies of MDH-A phenotypes were determined for 1125 beaked redfish examined from a winter survey in 1983 and 376 from a summer survey in 1984. Allele frequencies were calculated from the MDH-A phenotypic data for the winter survey. The low mobility of the A^2 phenotype was characteristic of 90% of *S. fasciatus* sampled at depths <320 m in winter and at depths <250 m in summer. The high-mobility A^1 and heterozygotic A^1/A^2 phenotypes were prevalent in 95% of *S. mentella* sampled below these depths. The mobility patterns agreed with predominant AFCs ($\leq$7 for *S. fasciatus* $\geq$8 for *S. mentella*) for all stations in the deep and shallow zones. The MDH mobility patterns showed 93% agreement with EGM patterns for *S. fasciatus* but only 53% agreement for *S. mentella*. An overlap of AFCs, of main EGM patterns, and of tendon to vertebrae attachments and the variation from set to set in A^1/A^2 heterozygotic phenotypes suggest that these species hybridize in the Gulf of St. Lawrence.

Les patrons de mobilité électrophorétique de la malate déshydrogénase (MDH) ont servi de référence à des méthodes de terrain utilisant le nombre de rayons de la nageoire anale (AFCs) et les patrons de passage transcostal du muscle extrinsèque de la vessie natatoire (EGM) ont été comparés afin de séparer les espèces de poissons rouges à protubérance, *Sebastes fasciatus* et *S. mentella*. Les fréquences des phénotypes de la MDH-A ont été déterminées pour 1 125 poissons rouges capturés lors d'un recensement effectué durant l'hiver 1983 et pour 376 spécimens provenant d'un recensement de l'été 1984. Les fréquences alléliques ont été calculées à partir des données phénotypiques pour la MDH-A lors du recensement d'hiver. La faible mobilité du phénotype A^2 était typique de 90 % des *S. fasciatus* échantillonnés à des profondeurs de < 320 m durant l'hiver et de < 250 m durant l'été. Les phénotypes de mobilité élevée A^1 et les hétérozygotes de mobilité intermédiaire A^1/A^2 prédominaient chez 95 % des *S. mentella* provenant de profondeurs plus grandes. Les patrons de mobilité concordaient avec les AFCs prédominantes ($\leq$ 7 pour *S. fasciatus*, $\geq$ 8 pour *S. mentella*) et ce, pour les sites de grande profondeur autant que pour ceux de faible profondeur. Les patrons de mobilité de la MDH affichaient une concordance de 93 % avec les patrons d'EGM pour *S. fasciatus* mais de seulement 53 % dans le cas de *S. mentella*. Un chevauchement dans les AFCs, dans les patrons du muscle EGM principal et dans les points d'ancrage des tendons aux vertèbres, de même que les fluctuations dans les phénotypes hétérozygotes A^1/A^2 d'un site à l'autre, indiquent que, dans le Golfe Saint-Laurent, ces espèces font l'objet d'hybridation.

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Three species of redfish, the Acadian redfish (*Sebastes fasciatus*), deepwater redfish (*S. mentella*), and golden redfish (*S. norvegicus*), occur in the Northwest (NW) Atlantic (Fernholm and Wheeler 1983; Scott and Scott 1988; McAllister 1990). They are difficult to separate on field surveys because of overlapping meristic and morphological characters. Whether the different types are distinct species or subspecies has been the subject of controversy. In recent years, studies using a combination of external meristic and/or morphological characters have been conducted (Barsukov 1972, Barsukov and Zakharov 1972; Ni 1981a, 1982, 1984; Kenchington 1983, 1986a; Misra and Ni 1983; Misra 1985; Power and Ni 1985). Most of these studies were successful in demonstrating differences between the types, lending support to the assertion that they are distinct species. However, in terms of fisheries management, no single character was identified that could provide an unambiguous separation of the species during surveys. It would be desirable to manage redfishes by species (Barsukov and Zakharov 1972), but this requires reliable means to separate them in the field.

Studies of internal morphological characters have indicated that beaked redfish species can be separated using extrinsic gasbladder muscle (EGM) passage patterns between the ventral ribs (Hallacher 1974; Litvinenko 1980; Ni 1981a). Hallacher compared main EGM patterns of 82 species of mostly Pacific rockfish, but also three specimens from the NW Atlantic, which in an addendum he termed *S. fasciatus*. Hallacher also presented EGM rib passage patterns determined by W. N. Eschmeyer for the three NW Atlantic species and *S. viviparus* from the eastern North Atlantic. Litvinenko (1980) described the shape, main EGM rib passage patterns, and tendon to vertebrae (TTV) insertion patterns from the branches of the EGM for the four North Atlantic redfish species. While the species allocations by Hallacher, Eschmeyer, and Litvinenko may be valid, they did not examine enough specimens to adequately define the variation in EGM rib passage patterns within species.

Ni (1981a) described EGM rib passage patterns and TTV insertion patterns for 100 *S. fasciatus* and 99 *S. mentella* specimens obtained from northeastern (NE) Grand Bank. In *S. fasciatus*, the main EGM passed between ventral ribs 3 and 4 in 94 fish and between ribs 4 and 5 for five fish. In *S. mentella*, the main EGM passed between ventral ribs 2 and 3 in 93 fish and was bifurcated around a rib in six redfish, with five having bifurcated branches between ribs 1 and 2 and 2 and 3. Ni proposed that main EGM patterns appeared to provide an unambiguous method to separate *S. fasciatus* from *S. mentella*.

Ni (1981b) determined that anal fin ray count (AFC) was the external meristic character that provided the greatest degree of separation between the beaked redfish species *S. fasciatus* and *S. mentella*. Specimens of these species sampled from the NE Grand Bank were found to have almost no overlap of AFCs. Unfortunately, there appears to be a greater degree of overlap of AFCs between these two species in other areas off the east coast of Canada (Ni 1982).

Circularity of reasoning may have been used in initially proposing main EGM patterns (Ni 1981a) and AFCs (Ni 1981b) as methods for separating *S. fasciatus* from *S. mentella* (Kenchington 1986a). Both of Ni's papers are based on the same specimens from NE Grand Bank. In the EGM paper (Ni 1981a) the specimens were preliminarily grouped on the basis of AFCs and depth. In the meristic characters paper (Ni 1981b), the specimens were initially separated into two groups using main EGM patterns. AFCs have overlapping distributions in all three NW Atlantic *Sebastes* spp. (Ni 1981b, 1984). The range of main EGM passages appears to be nonoverlapping but adjacent for *S. fasciatus* and *S. mentella* from NE Grand Bank (Ni 1981a) and intermediate in *S. norvegicus* from Flemish Cap and St. Pierre Bank off southern Newfoundland (Power and Ni 1982). The genetic basis of the EGM and AFC characters is unknown (McGlade et al. 1983).

Payne and Ni (1982) and McGlade et al. (1983) used electrophoresis coupled with histochemical staining to visualize and interpret protein banding patterns as gene products from a variety of allozyme loci. Those studies found differences between NW Atlantic redfish species in the protein mobility patterns of malate dehydrogenase (MDH) (EC 1.1.1.37). Two cytosolic loci, s*MDH-A** and s*MDH-B**, and one mitochondrial locus, m*MDH-A** (herein termed m*MDH-C** to avoid confusion with the cytosolic locus), are commonly found in diploid fishes (Buth 1983). Payne and Ni (1982) found that the s*MDH-A** locus was polymorphic with two alleles designated *A*1* and *A*2* determining the three MDH-A phenotypic patterns. Using liver samples, three phenotypic patterns were observed: a single low-mobility band pattern A^2, a single high-mobility band A^1, and a three-banded high-mobility pattern A^1/A^2 in specimens that were heterozygotes. The A^2 phenotype was predominant in *S. fasciatus* (79.6%), and the A^1 phenotypic pattern predominated in *S. mentella* (100%) and *S. norvegicus* (67.6%). *Sebastes fasciatus* and *S. norvegicus* from St. Pierre Bank exhibited all three phenotypic patterns, while five specimens of *S. mentella* from St. Pierre Bank and 31 from Hamilton Bank off Labrador had only the A^1 phenotype.

McGlade et al. (1983) found similar banding patterns in liver samples, for the three NW Atlantic species, taken from the Scotian Shelf off Nova Scotia. The specimens were initially identified using AFCs and other morphological characters. They found that *S. mentella* exhibited the three-banded A^1/A^2 heterozygotic pattern. Hence, all three species of NW Atlantic redfish can exhibit polymorphism at the *MDH-3** (herein termed s*MDH-A**) locus.

Differences in the relative mobilities of MDH phenotypic protein bands can provide a high degree of separation of *S. fasciatus* from either *S. mentella* or *S. norvegicus* (Payne and Ni 1982; McGlade et al 1983). Different allele frequencies between species result in the predominance of the low-mobility A^2 phenotypic band with *S. fasciatus* and the predominance of a more anodally displaced, higher mobility A^1 band with *S. mentella* and *S. norvegicus*. While there is overlap of MDH-A phenotypic patterns, the differences in relative frequencies can be used to separate the beaked redfish species *S. fasciatus* and *S. mentella* in the Gulf of St. Lawrence (Gulf).

Ni (1983) noted that redfish species distributions, stock units, and intraspecific geographic variation can only be tested on the same specimens by a combination of studies including examination of the EGM, biochemical population genetics, and meristics as done in the preliminary study of Payne and Ni (1982). Kenchington (1986a) proposed that field separation of *S. fasciatus* and *S. mentella* might be obtained using AFCs. He noted that before such a method could be applied, the appropriate ray counts, depths, and length ranges of each area would have to be determined using specimens identified by the electrophoretic technique of McGlade et al. (1983).

Sebastes mentella occurs in deeper water than *S. fasciatus*, based on a variety of morphometric and meristic characters (Barsukov and Zakharov 1972; Ni 1982). One can predict from this that main EGM passage patterns and AFCs should differ

by depth, according to the different depth zones occupied by each beaked redfish species. Consequently, this study has examined MDH mobility patterns, AFCs, and EGM patterns with trawl sets arranged according to increasing depth.

The present study was conducted to evaluate main EGM passage patterns (Ni 1981a) and AFCs (Ni 1981b) as field methods to identify sets according to beaked redfish species on research vessel surveys. The hypothesis being tested was that each method when compared with MDH mobility patterns should agree with species identifications from set to set. MDH mobility patterns, because they consist of dimeric proteins transcribed from a few alleles, have an explicable genetic basis. Hence, they were considered to be the most reliable method for identifying beaked redfish species. MDH patterns were chosen as the standard against which the field identification methods were compared.

This paper is divided into four parts. A genetic analysis of MDH mobility patterns in the Gulf is conducted in Part I; Part II examines between-set variation of EGM and TTV patterns and compares EGM and MDH patterns; Part III compares the agreement between AFCs and MDH mobility patterns; Part IV compares EGM, TTV, and AFC patterns between the Gulf and other areas.

Material and Methods

Redfishes were sampled for meristic data and tissues for biochemical analyses during two research vessel surveys in the Gulf. During the January 1983 cruise, on the *Gadus Atlantica*, 1142 redfish were sampled at 23 stations. On the *Lady Hammond*, 695 redfish were sampled in July 1984 at 25 stations. Most of the redfish sampled had a well-developed beaklike fleshy protuberance on the lower jaw (schnabel) indicating that they were beaked redfishes (Barsukov 1972; Ni 1984). The beaked redfishes *S. fasciatus* and *S. mentella* were fairly easy to separate from *S. norvegicus*, which had a blunt schnabel and a more stout body shape (Templeman and Sandeman 1957; Power and Ni 1985). Notes were made on the labels of redfish that resembled *S. norvegicus* because it has AFCs similar to *S. mentella* (Ni 1984). The former species was rare in the catch and was found in the shallow depth zone (100–250 m) along with *S. fasciatus*. Hence, *S. norvegicus* was separable from the beaked redfish species, at least with larger specimens. Juvenile golden redfish were more difficult to identify, and some may have been misidentified as *S. mentella* on the surveys. Most of the redfish sampled for biochemical analyses from both surveys were adults (> 20 cm) and were easily identified as beaked redfishes. Because *S. norvegicus* was rarely taken (< 1% of catch), it was not believed to bias the interpretation of methods being evaluated for the separation of the beaked redfish species.

MDH mobility patterns can only be used to separate beaked redfish species on sets where *S. norvegicus* is not present, or after it has been sorted from the catch using its golden colour, blunt schnabel, and other external morphological characters (Templeman and Sandeman 1957). In the present analysis, specimens which morphologically appeared to be *S. norvegicus* (2 from set 140, 15 from set 173 on the winter survey, and 8 from set 4 on the summer survey) were excluded from the data.

On both the winter and summer surveys, redfish were sampled at random from the catch and their AFCs recorded at randomly chosen localities in the Gulf. Counts were made on the soft anal rays, excluding the first three fin spines. The last two soft rays, which arise close together from the same pterygiophore, were counted as one. The 1125 beaked redfish sampled for liver tissue and AFCs on the winter survey were discarded after being sampled. Of 687 beaked redfish from which AFCs were taken on the summer survey, 376 were sampled for liver and muscle tissues for biochemical analyses. The whole fish were also frozen in plastic bags.

In Moncton, N.B., 321 beaked redfish specimens from the summer survey were dissected to determine EGM passage patterns, according to procedures described by Hallacher (1974) and Ni (1981a). The passages off the main EGM, or its main bifurcations, and small branches off the EGM were determined. For each fish, the main EGM and small muscle branches were enumerated and their rib passages determined. TTV insertions were recorded for 244 of these redfish. Morphometric characteristics such as the shape of the EGM, the degree of development of the schnabel, and pointed shape of the preopercular spines were also noted. Notes were taken from 42 redfish regarding the angle of the head above the eyes, pigment patterns behind the eye, body shape, and body colour (Templeman and Sandeman 1957; Power and Ni 1985).

To verify EGM patterns, 126 of the dissected fish were reexamined several months later and scored for main and small EGM rib passage patterns, without reference to the previous data. The information was then compared to evaluate the reproducibility of the interpretations. The 42 specimens, taken from the second sample, were examined a third time by Dr. I-H. Ni (Northwest Atlantic Fisheries Centre, St. John's, Nfld.) to compare his interpretation with our own. Of the dissected specimens, 25 have been preserved and donated to the Canadian Museum of Nature in Ottawa, Ont. (Catalogue Nos. NMC89-0209, NMC89-0210).

The raw data from each set for EGM passage and TTV insertion patterns were tested for heterogeneity between sets within species by means of the Kruskal–Wallis test (SAS Institute Inc. 1987). The set totals for each species were compared between the Gulf and NE Grand Bank, within each species, and between *S. fasciatus* and *S. mentella*, using the Mann–Whitney–Wilcoxon two-sample test.

During the surveys, about 5–10 g of skeletal muscle from the dorsal left side and 5 g of liver tissue was removed from each redfish and separately frozen in plastic bags. Liver and muscle samples from the summer survey were analyzed at Université de Moncton as described by McGlade et al. (1983). The differences in MDH cytosolic electrophoretic protein band patterns between these tissues were examined.

Liver samples from the winter survey were analyzed at the Bedford Institute of Oceanography, Dartmouth, N.S., using starch-gel electrophoresis as described by McGlade et al. (1983). The MDH protein mobility patterns from both the winter and summer surveys were scored, using the phenotypic notation of Payne and Ni (1982). Homomeric and heteromeric protein nomenclature is adopted from Utter et al. (1987). The genetic nomenclature is consistent with Shaklee et al. (1990).

The respective predominances of the A^2 or A^1 phenotypic patterns, with redfish taken on separate sets, were used to identify *S. fasciatus* and *S. mentella* by trawl set. The A^1/A^2 phenotype was considered indicative of the presence of *S. mentella* on sets where the A^1 pattern predominated. Conversely, when the A^2 pattern predominated on a set, the A^1/A^2 phenotype was considered indicative of the presence of *S. fasciatus* because of genetic polymorphism (Payne and Ni 1982).

To test species uniformity by set, the observed and expected genotypic frequencies were tested for Hardy–Weinberg equi-

libria, using the *G* statistic of Sokal and Rohlf (1969). The *G* statistic for replicated tests of goodness of fit was used to assess heterogeneity of genotypes among populations between sets, within each redfish species. The relative frequencies of the *A*1* and *A*2* alleles by set were calculated for the two beaked redfish species from the Hardy–Weinberg formula as outlined by Ferguson (1980). Allele frequencies were compared for heterogeneity between sets with each redfish species using a two-way contingency *G* test of independence (Sokal and Rohlf 1969). The simultaneous test procedure (STP) was used to determine the grouping of trawl sets with similar allele frequencies. *MDH-A** genotype and allele frequencies, AFC, and EGM frequencies determined in the Gulf have been compared with those in other areas (Ni 1981a; Payne and Ni 1982).

Results

Part I. Genetic Analysis of MDH Mobility Patterns

MDH mobility patterns

Utter et al. (1987) discussed electrophoretic patterns where the same type of protein is encoded by two loci. MDH is a dimeric protein formed under the control of one cytosolic locus (*A**) which is polymorphic (with alleles *A*1* and *A*2* resulting in protein subunits a^1 and a^2, respectively) and a second locus (*B**) which is monomorphic coding for a subunit (b) with an electrophoretic mobility that differs from subunits a^1 and a^2. With liver samples, the banding patterns are only expressed from the *MDH-A** locus, and three dimeric protein bands are possible (Fig. 1). Banding patterns with muscle tissue are expressed from both s*MDH-A** and s*MDH-B** loci. The MDH proteins can consist of combinations of the b subunit from the second locus and the a^1 or a^2 subunit from the first locus. The *A1A1BB** and *A2A2BB** genotypes with muscle each transcribe three dimeric protein bands composed of paired combinations of a^1,b subunits, or a^2,b subunits, respectively.

Six dimeric protein bands for muscle tissue from the s*MDH-A** and s*MDH-B** loci are theoretically possible, representing paired combinations of the subunits a^1, a^2, and b, expressed from the *A1A2BB** heterozygote (Fig. 1). However, the a^1b and a^2a^2 bands have similar mobilities which produce one visible protein band, and the a^2b and bb bands also overlap producing one visible band. Hence, four distinct bands were visible on the gels from muscle samples with the heterozygotic pattern.

Liver and muscle samples from the same redfish, run on separate tracks of the same gel, showed the most anodally displaced a^1a^1 protein band for liver in line with the a^1a^1 band obtained with the muscle samples (Fig. 2). The a^2a^2 band in the liver samples had the same mobility as the a^2a^2 and a^1b bands in the muscle samples. Muscle samples exhibited a distinct band (bb), situated below the previously mentioned bands, that was not present in the liver protein banding patterns (Fig. 3). When a three-banded heterozygotic phenotypic pattern was observed with a liver sample, an additional protein band (a^1a^2) was noted between the two most anodally displaced bands of the matching muscle sample taken from the same fish (see fish 1030).

A faint band was also visible at the bottom of both muscle and liver gels near the origin (Fig. 2 and 3), which was believed to represent a dimeric protein (cc) expressed off the m*MDH-C** locus.

Phenotypic frequencies from winter survey

At depths from 132 to 315 m, of a total sample of 625 fish, 89.8% exhibited the low-mobility A^2 phenotypic pattern, 1.6% the high-mobility A^1 pattern, and 8.6% the three-banded heterozygotic A^1/A^2 pattern (Table 1). At 320 m, a sample of 50 fish exhibited the following phenotypic frequencies: 52% A^2, 26% A^1, and 22% A^1/A^2. From a total sample of 450 redfish at greater depths (355–444 m), 71.3% exhibted A^1, 2.4% A^2,

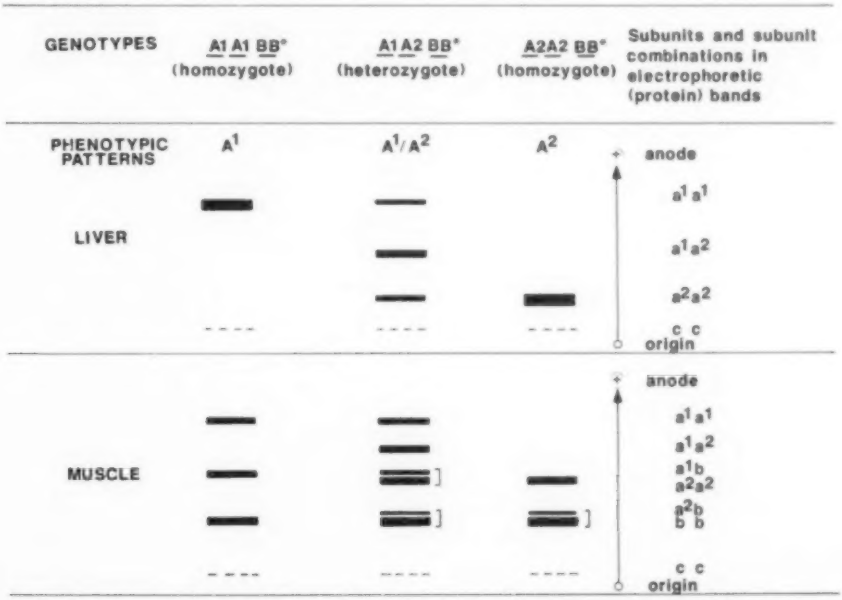

FIG. 1. Comparison of MDH phenotypic protein banding patterns observed in redfish for liver and muscle samples expressed under the control of two loci, one of which (*A**) is polymorphic and the second (*B**) is monomorphic.

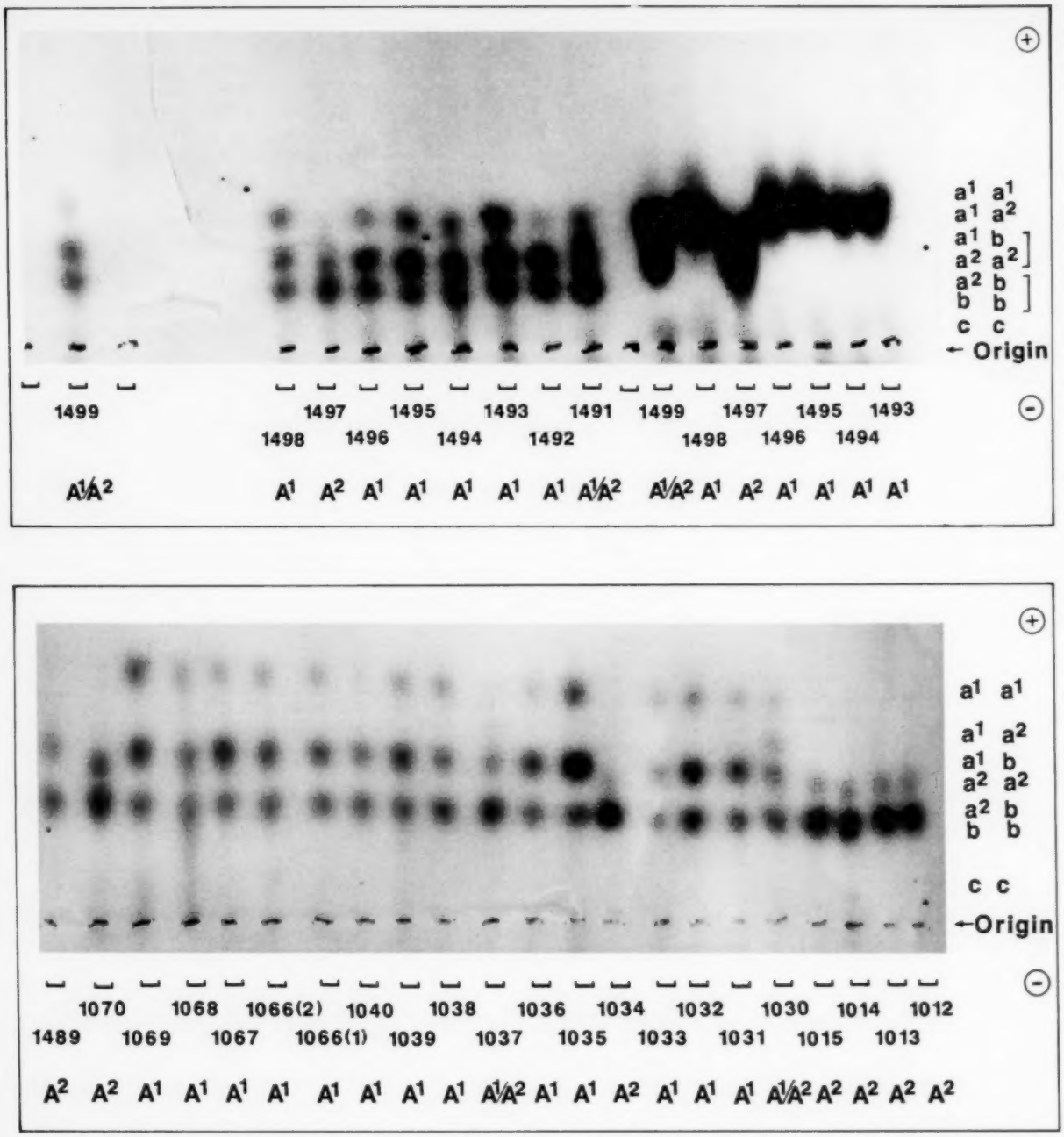

FIG. 3. MDH protein banding patterns exhibited with muscle samples from *S. fasciatus* (samples 1012–1015) and *S. mentella* (samples 1030–1040, 1066–1070, and 1489).

and 26.2% the A^1/A^2 pattern. There was a large variation for each phenotype between sets.

Genotypic frequencies

Using the Hardy–Weinberg formula, observed and expected genotypic frequencies (Table 2) were calculated for each set sampled on the winter survey. Nonsignificant *G* statistics indicated that most sets within each species had stable Hardy–Weinberg equilibria. Sets 13 and 165 in the shallow zone had significant *G* values due to a deficiency of heterozygotes. Likewise, set 184 in the deep zone had a highly significant *G* value due to a deficiency of heterozygotes. The *G* value for set 18 was significant due to a surplus of observed heterozygotes. The pooled *G* values for the shallow and deep zone, respectively, were also significant and exhibited a deficiency of heterozygotes.

TABLE 1. Number and relative frequency of MDH-A phenotypic patterns determined from redfish sampled on the winter survey.

Mean depth (m)	Set No.	No. of fish	Phenotype A^2, 1 bottom band	Phenotype A^1, 1 top band	Phenotype A^1/A^2, 3 bands
132	22	48	48 (100)	0 (0)	0 (0)
160	174	50	41 (82)	0 (0)	9 (18)
162	173	35[a]	35 (100)	0 (0)	0 (0)
196	56	50	50 (100)	0 (0)	0 (0)
208	163	50	48 (96)	1 (2)	1 (2)
236	140	48[b]	39 (81)	1 (2)	8 (17)
236	153	47	47 (100)	0 (0)	0 (0)
243	36	54	50 (93)	0 (0)	4 (7)
243	88	48	36 (75)	0 (0)	12 (25)
247	31	49	42 (86)	0 (0)	7 (14)
276	95	50	49 (98)	1 (2)	0 (0)
285	13	50	40 (80)	3 (6)	7 (14)
315	165	46	36 (78)	4 (9)	6 (13)
Total		625	561 (89.8)	10 (1.6)	54 (8.6)
320	184	50	26 (52)	13 (26)	11 (22)
355	177	61	1 (1)	45 (74)	15 (25)
364	169	50	2 (4)	37 (74)	11 (22)
371	176	50	2 (4)	38 (76)	10 (20)
395	18	50	0 (0)	31 (62)	19 (38)
422	130	50	2 (4)	40 (80)	8 (16)
427	164	49	1 (2)	27 (55)	21 (43)
440	10	49	0 (0)	37 (76)	12 (24)
443	167	45	3 (7)	32 (71)	10 (22)
444	3	46	0 (0)	34 (74)	12 (26)
Total		450[c]	11 (2.4)	321 (71.3)	118 (26.2)

[a]Excluding 15 *S. norvegicus*.
[b]Excluding two *S. norvegicus*.
[c]Not including set 184.

Interpopulation comparisons of total, pooled, and heterogeneity G values found that the pooled G value for all the sets in the shallow zone was highly significant, while the heterogeneity G value was nonsignificant (Table 3). The pooled G value became nonsignificant when sets 13 and 165 were excluded from the calculations. The sets in the deep zone exhibited significant total and pooled G values and a nonsignificant heterogeneity G value. The total and pooled G values became nonsignificant when sets 18 and 184 were excluded from the calculations.

Allele frequencies

The A^*2 allele predominated in the shallow zone, with frequencies ranging from 0.85 to 1.00 (Table 4). This was markedly different from the deep zone where the A^*1 allele predominated with frequencies ranging from 0.77 to 0.88.

The variability of allele frequencies (Table 4), from set to set, raised the question as to whether the variation was due to genetic variability within species or to the infrequent occurrence of *S. mentella* with *S. fasciatus* in the shallow zone or vice versa in the deep zone. The STP test indicated that A^* allele frequencies for the sets in the shallow zone were significantly heterogeneous ($G = 77.95$, $\chi^2 = 21.03$, 12 df, $P < 0.05$). Partitioning and grouping of the data indicated that sets 22, 173, 56, 153, 95, and 163 formed a homogeneous nonsignificant group and that sets 36, 174, 31, 140, 88, 13, and 165 formed a second nonsignificant grouping. The first group was marked by the predominance of the A^*2 allele (frequencies > 0.96) and (with the exception of one fish from set 163) the absence of observed heterozygotes (Table 1). The second grouping (Table 4) had a lower frequency of the A^*2 allele (frequency range 0.85–0.96) and heterozygotes present for all sets. Hence, two groups of *S. fasciatus* were noted in the shallow zone, marked by the presence or absence of heterozygotes. The STP G test indicated that the sets in the deep zone, excluding set 184, formed a homogeneous grouping with respect to allele frequencies.

Part II. Variation and Comparison of EGM, TTV, and MDH Patterns

Comparison between EGM group and MDH patterns

The main EGM or its branches often pass between the same pair of ribs, or bifurcate around a rib to pass between two pairs of ribs. Main EGM rib passage patterns (E), with 212 beaked redfish taken on the summer survey (A, Table 5), were found to pass between ribs 3 and 4 and/or 4 and 5, in a manner characteristic of *S. fasciatus* (Ni 1981a). The main muscle in this "Fasciatus" group (A, Table 5) passed between ribs 3 and 4 (178 fish) or between ribs 4 and 5 (14 fish). Seven fish had a bifurcated main EGM between ribs 3 and 4, and 13 a bifurcated EGM which passed between ribs 3 and 4 and 4 and 5. The MDH biochemistry showed that 123 (58%) of these redfish had the low-mobility A^2 pattern, but this left 89 (42%) with higher mobility (A^1 and A^1/A^2) patterns.

Main EGM passages between ribs 2 and 3, or 2 and 3 and 3 and 4 occurred with 109 beaked redfish termed the "Mentella" group (B, Table 5) (Ni 1981a). The high (A^1 and A^1/A^2) protein mobility patterns agreed with these rib passage patterns for 101 redfish (93%). However, there were eight (7%) of the fish with Mentella rib passage patterns which had the low A^2 mobility pattern.

The small muscles branching off the main EGM exhibited similar rib passage patterns to those described by Ni (1981a). In the Fasciatus group, most small muscles passed between ribs 2 and 3, and a smaller number passed between ribs 3 and 4 or 4 and 5. In the Mentella group, most small muscles passed between ribs 2 and 3, with fewer passing between ribs 1 and 2 or 3 and 4. The number of small muscles varied from one to three for both the Fasciatus and the Mentella groups. Ni (1981a) found one to three small muscle branches in *S. fasciatus*, but only one small muscle branch off the main EGM in *S. mentella*.

A comparison of main EGM with MDH mobility patterns indicated a high proportion of both A^1 and A^2 mobility patterns for the Fasciatus group, particularly for the 3–4 passage (Table 6). There was also a high proportion of the A^1/A^2 phenotype. The relative proportion of the A^2 phenotype (58.0%) was lower, and the relative frequencies of the A^1 (26.4%) and A^1/A^2 (15.6%) phenotypes in the Gulf were higher than those found with *S. fasciatus* (79.6% A^2, 6.8% A^1, and 13.6% A^1/A^2) on St. Pierre Bank (Payne and Ni 1982). For the Mentella group, all three phenotypes occurred in the Gulf. The relative frequency of the A^1 phenotype (78.9%) was lower than that found with *S. mentella* from Hamilton Bank (100%) by Payne and Ni (1982). Lower proportions for the relative frequencies of A^1 or A^2 phenotypes (Tables 5 and 6) were found in the Gulf according to putative redfish species, with the specimens classified by means of main EGM passage patterns, similar to Payne and Ni (1982).

TABLE 2. Comparison of observed and expected (in parentheses) genotypic frequencies according to the Hardy–Weinberg formula at the *MDH-A** locus for *S. fasciatus* and *S. mentella* sampled at various localities during the winter survey in the Gulf of St. Lawrence.

Set No.	No. of fish	Genotype			G	$P < 0.05$
		*A2A2**	*A1A2**	*A1A1**		
22	48	48 (48.0)	0 (0.0)	0 (0.0)	0.0000	
174	50	41 (41.4)	9 (8.2)	0 (0.4)	0.8795	
173	35	35 (35.0)	0 (0.0)	0 (0.0)	0.0000	
56	50	50 (50.0)	0 (0.0)	0 (0.0)	0.0000	
163	50	48 (47.0)	1 (2.9)	1 (0.0)	−0.1082	
140	48	39 (38.0)	8 (9.4)	1 (0.6)	0.4675	
153	47	47 (47.0)	0 (0.0)	0 (0.0)	0.0000	
36	54	50 (49.8)	4 (4.1)	0 (0.1)	0.2033	
88	48	36 (36.8)	12 (10.5)	0 (0.8)	1.6224	
31	49	42 (42.4)	7 (6.4)	0 (0.2)	0.4584	
95	50	49 (48.0)	0 (2.0)	1 (0.0)	2.0207	
13	50	40 (37.8)	7 (11.3)	3 (0.8)	5.7518	*
165	46	36 (33.2)	6 (11.7)	4 (1.0)	8.9062	*
Pooled total	625	561 (552.3)	54 (70.5)	10 (2.3)	18.1342	*
184	50	26 (19.8)	11 (23.3)	13 (6.8)	14.5021	*
177	61	1 (1.2)	15 (14.7)	45 (45.1)	0.0416	
169	50	2 (1.1)	11 (12.8)	37 (36.1)	0.8797	
176	50	2 (1.0)	10 (12.0)	38 (37.0)	1.1530	
18	50	0 (1.8)	19 (15.4)	31 (32.8)	4.4834	*
130	50	2 (0.7)	8 (10.6)	40 (38.7)	2.3398	
164	49	1 (2.6)	21 (17.4)	27 (29.1)	3.6624	
10	49	0 (0.7)	12 (10.3)	37 (37.9)	1.8879	
167	45	3 (1.5)	10 (13.3)	32 (30.3)	1.9488	
3	46	0 (0.8)	12 (10.4)	34 (34.8)	1.8530	
Pooled total	500	37 (20.6)	129 (161.8)	334 (317.6)	18.5354	*

TABLE 3. Interpopulation comparisons of goodness of fit to Hardy–Weinberg of *MDH-A** genotypic frequencies for total, pooled, and heterogeneity G values calculated for redfish sampled from shallow and deep zones in the Gulf of St. Lawrence.

Depth zone	G value	$P<0.05$	df	G value	$P<0.05$	df
Shallow						
Total	20.2016[a]	NS	13	5.6973[b]	NS	11
Pooled	18.1342	*	1	2.9480	NS	1
Heterogeneity	2.0674	NS	12	2.7493	NS	10
Deep						
Total	32.7517[c]	*	10	13.7662[d]	NS	8
Pooled	18.5354	*	1	0.2774	NS	1
Heterogeneity	14.2163	NS	9	13.4888	NS	7

[a]All sets from 132 to 315 m.
[b]Excluding sets 13 and 165.
[c]All sets from 320 to 444 m.
[d]Excluding sets 18 and 184.

EGM passages by increasing depth

The relative frequencies of Fasciatus group "F" and Mentella group "M" main EGM patterns (Table 7), presented by set according to increasing depth, characterized fish fairly well in the shallow depth zone (99–248 m). There was a predominance of "F" EGM patterns for 9 out of 12 sets. The "M" pattern predominated on set 26, and there was about an equal proportion of both patterns for sets 20 and 54. In the deep zone (256–480 m), no clear pattern was observed. The EGM patterns varied in importance from set to set between the "F" and "M" groups. There were 46% "F" and 54% "M" EGM patterns present in the deep zone. These data might be interpreted as indicating that about equal proportions of the two species of beaked redfish occurred in the deep zone. However, this interpretation was rejected on the basis of predominant MDH mobility patterns.

MDH mobility patterns by depth

One can classify all beaked redfish on a set to one species, identified on the basis of the predominant MDH mobility pattern, if the remaining specimens with other MDH phenotypes are considered to be that species due to polymorphism (Table 7). Of 168 redfish sampled from 12 sets in the shallow depth zone (99–248 m), 126 (75%) had the A^2 band pattern and 42 (25%) had high-mobility (A^1 and A^1/A^2) patterns. For most shallow zone sets the A^2 pattern predominated. However, the A^1 pattern predominated with redfish from sets 26, 52, and 54. Most of the 42 fish with high-mobility patterns came from these latter sets. Excluding sets 26, 52, and 54, the A^2 pattern was found with 95% of the redfish from the remaining *S. fasciatus* (F) sets, classified on the basis of MDH-A polymorphism (Payne and Ni 1982). Combining sets 26, 52, and 54 with those from the deep zone, high-mobility patterns were found with 94% of the fish from these *S. mentella* (M) sets.

The polymorphism criterion was used to classify specimens which had mobility patterns different from the dominant pattern on each set (Table 7). Six redfish in the shallow zone from sets 15, 28, and 48 with high-mobility patterns were classified as

TABLE 4. Allele frequencies from set to set for redfish sampled at various localities and depths during the winter survey in the Gulf of St. Lawerence.

Set No.	Mean depth (m)	Alleles A^*2	Alleles A^*1	% heterozygosity per locus, $H_L = H_{obs.} - H_{exp.}$
		S. fasciatus		
22	132	1.00	0.00	0
173	162	1.00	0.00	0
56	196	1.00	0.00	0
153	236	1.00	0.00	0
95	276	0.98	0.02	−4
163	208	0.97	0.03	−4
36	243	0.96	0.04	0
31	247	0.93	0.07	1
174	160	0.91	0.09	2
140	236	0.90	0.10	−1
88	243	0.88	0.12	4
13	285	0.87	0.13	−9
165	315	0.85	0.15	−12
Pooled	132–315	0.94	0.06	−3
184	320	0.63	0.37	−25
		S. mentella		
164	427	0.23	0.77	7
18	395	0.19	0.81	7
167	443	0.18	0.82	−7
169	364	0.15	0.85	−4
176	371	0.14	0.86	−4
177	355	0.14	0.86	1
3	444	0.13	0.87	3
130	422	0.12	0.88	−5
10	440	0.12	0.88	3
Pooled[a]	355–444	0.16	0.84	−1

[a]Not including set 184.

S. fasciatus. Similarly, six redfish exhibiting the A^2 pattern from sets 52 and 54, where the A^1 pattern predominated, were classified as *S. mentella*. In the deep zone, five fish from sets 11, 25, 41, and 47 with the A^2 phenotype were considered to be *S. mentella*. All beaked redfish from sets where the low-mobility A^2 phenotype predominated were considered to be *S. fasciatus*, and all sets where most redfish had high-mobility patterns (A^1 + A^1/A^2) were interpreted to be *S. mentella*.

Agreement between EGM passages and MDH mobility patterns

Fasciatus group EGM patterns agreed by 95% with the A^2 mobility pattern for the 12 sets in the shallow zone (Table 7). Only 50% of 42 fish with high-mobility patterns had EGM group patterns which agreed. For 148 fish from the deep zone, 54% had Mentella group EGM patterns in agreement with the high-mobility patterns. Two of the remaining five fish (40%) had main EGM patterns in agreement with the A^2 mobility patterns.

For the deep and shallow zones combined, there was good agreement between the MDH mobility patterns and the main EGM passage patterns for fish which the biochemistry indicated to be *S. fasciatus* and poor agreement for *S. mentella* (Table 7). For *S. fasciatus*, 93% of 131 fish had EGM passages in agreement with the biochemistry. For *S. mentella*, only 53% of 190 fish had main EGM passage patterns in agreement with MDH mobility patterns. Even at the greatest depths, a high proportion of fish, which the high-mobility patterns indicated to be *S. mentella*, had Fasciatus group EGM rib passage patterns.

TABLE 5. Comparison between redfish EGM passage patterns (E = main; s = small) and MDH protein mobility patterns.

EGM passages between ventral ribs: 1–2	2–3	3–4	4–5	Biochemistry (MDH): Low-mobility pattern, A^2	High-mobility patterns, $A^1 + A^1/A^2$	Total
(A) "Fasciatus" group						
		E		10	4	14
		Es		14	5	19
	s	E		31	36	67
	ss	E		8	22	30
	s	Es		20	9	29
		Ess		3		3
	s	E	s	2		2
		Es	s	2		2
	sss	E		1	3	4
	ss	Es		2	1	3
	s	Ess		2		2
	s	Es	s	3		3
			E	1		1
		s	E	6	1	7
	s	s	E	1		1
		ss	E	4		4
	s	ss	E	1		1
		EE			1	1
	s	EE			2	2
	ss	EE		1	3	4
		E	E	1		1
		Es	E	2		2
	s	E	E	1		1
	ss	E	E	2	1	3
	s	Es	E	4		4
		Ess	E	1		1
	s	Ess	E		1	1
Total				123	89	212
(B) "Mentella" group						
		E		3	16	19
		Es		4	44	48
s		E			4	4
		Ess			14	14
		ES	s		4	4
s		Es			2	2
		Ess	s		1	1
s		Ess			1	1
		EEss		1	1	2
		E	E		2	2
		Es	E		5	5
		Ess	E		6	6
		EEs	E		1	1
Total				8	101	109
Grand total				131	190	321

Verification of EGM passages

Main EGM patterns were reexamined. There was 94% agreement, in comparison with the first examination, between the

TABLE 6. Summary of number of beaked redfish with main (=E) EGM passage patterns in relation to MDH-A mobility patterns.

Main rib passages between ventral ribs:				Biochemistry (MDH)			
				Low-mobility pattern,	High-mobility patterns		
1–2	2–3	3–4	4–5	A^2	A^1	A^1/A^2	Total
"Fasciatus" group							
		E		98	53	27	178
			E	13	1	0	14
		EE		1	2	4	7
		E	E	11	0	2	13
Total				123	56	33	212
"Mentella" group							
	E			7	73	13	93
	EE			1	1	0	2
	E	E			12	1	13
	EE	E			0	1	1
Total				8	86	15	109
Grand total				131	142	48	321

EGM patterns recorded for 126 beaked redfish which were examined twice. The minor discrepancies in the interpretation of EGM patterns could not account for the high agreement between biochemistry and EGM data for *S. fasciatus* and the low agreement with *S. mentella*. Even at the deepest stations, 47% of *S. mentella* had Fasciatus group main EGM patterns (Tables 6 and 7). These fish were *S. mentella* based on the biochemistry, external pigment patterns, pointed schnabel, and low angle of the head. It must be concluded that the 3–4 EGM passage pattern was prevalent with both *S. fasciatus* and *S. mentella* in the Gulf.

Of the dissected redfish examined by Ni, 42 had matching biochemical data. MDH mobility patterns indicated that there were 21 *S. fasciatus* and 21 *S. mentella* in the sample. For *S. fasciatus*, both our EGM species identifications and those of Ni were in 100% agreement with A^2 mobility patterns. Out of the 21 *S. mentella*, our EGM patterns agreed for 47% with high MDH mobility patterns. Ni used the shape of the main EGM (thicker and longer in *S. fasciatus* than with *S. mentella*) and the angle of the head in addition to main EGM rib passage patterns to make his identifications. With the *S. mentella* sample, 62% of Ni's determinations agreed, and 38% could not be matched with the A^1 and A^1/A^2 mobility patterns. While Ni's identifications were closer to the biochemical standard than our own, they also indicated that EGM passage patterns could not reliably identify *S. mentella* in our Gulf sample.

Between-set variation of EGM and TTV patterns

The relative frequency of main EGM passages and TTV insertions for main and small muscles off the EGM were summarized for 244 redfish from which detailed dissections and MDH mobility data were obtained (Table 8). According to MDH-A mobility patterns, there were 108 beaked redfish with the A^2 phenotype and 136 with the A^1 or A^1/A^2 phenotype. After 11 redfish specimens were reclassified to the dominant species on the set because of genetic polymorphism, there were 109 *S. fasciatus* and 135 *S. mentella*. The TTV insertions exhibited a large variation in attachments to vertebrae between individual redfish at a given location. There also appeared to be differences in the TTV distributions, from set to set, for each redfish species.

Part III. AFC Variation and Comparison with MDH Mobilities

AFCs by increasing depth

The AFC and biochemical data from the winter survey for each sampling locality have been arranged according to increasing depth (Table 9). In the shallow depth zone (132–315 m), 79% (range 62–90) of the redfish from the various sets had AFCs ≤ 7. The majority of these fish (mean 90%, range 75–100) exhibited the low-mobility A^2 pattern. In the deep zone (355–444 m), 88% (range 66–96) of the redfish from the various sets had AFCs ≥ 8. The majority of redfish in the deep zone (mean 98%, range 93–100) had high-mobility (A^1 + A^1/A^2) phenotypic patterns.

The relative frequencies of AFCs according to MDH-A phenotypic patterns (Fig. 4) were compared for redfish from the deep and shallow zone, respectively, on the winter survey. In the shallow zone, redfish exhibiting the A^2 phenotype had an AFC mode of 7, while A^1/A^2 heterozygotes had an AFC mode of 8. The few fish with the A^1 phenotype had about equal proportions of 7 or 8 AFCs. In the deep zone, the A^1 and A^1/A^2 phenotypic patterns had similar AFC frequency distributions with modes of 8. The fish with the A^2 phenotype also had a mode at 8, but there was a higher proportion of fish with AFCs of 7 than noted for the other phenotypes.

On the summer survey (Table 10), 77% (range 60–93) of the redfish sampled on 9 out of 12 sets, from a shallow depth range of 99–248 m, had AFCs ≤ 7. These fish exhibited predominantly the low-mobility A^2 pattern (mean 95%, range 80–100). Sets 26, 52, and 54 differed in this respect with 91% (range 84–100) of the redfish exhibiting AFCs ≥ 8 and the MDH results indicating high-mobility (A^1 + A^1/A^2) patterns predominating (mean 87%, range 73–100).

Redfish sampled (Table 10) from sets in deeper water (256–480 m) on the summer survey had AFCs which were predominantly ≥ 8 (mean 91%, range 76–100). High-mobility patterns (A^1 + A^1/A^2) predominated (mean 97%, range 87–100) for the redfish on all 13 sets sampled from the deep zone. The transition depth, between the two types of redfish with differing AFCs, was deeper during the winter (320 m) than during the summer (250 m) (Tables 9 and 10).

60% AFC rule

Based on the MDH mobility data presented (Tables 9 and 10), a 60% AFC rule was adopted to assign all the redfish on most sets to one or the other of the two beaked redfish species for the winter and the summer surveys. The MDH data indicated that there was a greater than 90% probability that when 60% or more of the AFCs on a trawl set were ≤ 7, the redfish should all be *S. fasciatus*. Similarly, when 60% or more of the AFCs were ≥ 8 on a set, the redfish could be considered to be *S. mentella*. When the proportion of AFCs was between 40 and 60% for both counts ≤ 7 and ≥ 8, it was assumed that there were two species of redfish present. The geographic distribution patterns of each species by trawl sets are depicted for the winter (Fig. 5) and summer survey (Fig. 6) using this method of classification.

TABLE 7. Comparison of agreement between relative frequencies of EGM patterns with species interpretations from MDH biochemistry by depth. "F" = Fasciatus EGM patterns, "M" = Mentella EGM patterns, F = *S. fasciatus*, M = *S. mentella*.

Mean depth (m)	Set No.	No. of fish matching data	% EGM		% MDH		MDH and EGM % agreement		Species allocation	
			"F"	"M"	A^2	A^1+A^1/A^2	"F"	"M"	F	M
99	20	2	50	50	100	0	50		100	0
170	36	15	100	0	100	0	100		100	0
177	28	15	100	0	93	7	93	0	100	0
182	48	15	93	7	87	13	100	50	100	0
183	40	14	93	7	100	0	93		100	0
199	52	15	67	33	27	73	100	45	0	100
205	42	15	100	0	100	0	100		100	0
213	4	20[a]	80	20	100	0	80		100	0
233	54	15	53	47	13	87	100	53	0	100
242	30	15	100	0	100	0	100		100	0
246	26	12	33	66	0	100		67	0	100
248	15	15	100	0	80	20	100	0	100	0
256	41	14	57	43	7	93	100	46	0	100
273	23	14	36	64	0	100		64	0	100
283	47	5	40	60	20	80	0	50	0	100
283	25	15	33	67	7	93	0	64	0	100
285	46	12	67	33	0	100		33	0	100
288	32	4	50	50	0	100		50	0	100
300	44	15	53	47	0	100		47	0	100
304	11	15	33	67	13	87	50	69	0	100
351	9	23	43	57	0	100		57	0	100
434	3	9	44	56	0	100		56	0	100
464	6	8	50	50	0	100		50	0	100
473	17	14	36	64	0	100		64	0	100
480	1	5	80	20	0	100		20	0	100
99–248		168	84	16	75	25	95	50	75	25
256–480		153	46	54	3	97	40	54	0	100
	F sets	126	94	6	95	5	95	17	100	0
	M sets	195	47	53	6	94	73	54	0	100
All depths		321	66	34	41	59	93	53		

[a]Excluding eight *S. norvegicus* specimens.

Set 184 on the winter survey (Table 9) should be considered as evidence for a transition zone, since the MDH-A mobility data indicated a half and half occurrence of *S. fasciatus* and *S. mentella* at the 320-m interface between the two depth zones. Using the interpretation of Payne and Ni (1982), concerning the differences in relative frequency of MDH-A phenotypic banding patterns between beaked redfish species, the winter and summer survey results (Tables 7, 9, and 10) indicate that *S. fasciatus* and *S. mentella* mostly occupied separate depth zones.

AFC data from the summer survey, including sets which were not tested biochemically, were classified to one or the other beaked redfish species using the 60% AFC rule (Table 11). Using this criterion, 92 out of 93 sets were allocated to *S. fasciatus* (F) or *S. mentella* (M). AFCs from set 33 which did not meet the 60% ≤7 or 60% ≥8 criterion were designated (?). The data indicated that AFCs ≤7 characteristic of *S. fasciatus* predominated at depths between 112 and 239 m, while AFCs ≥8 characteristic of *S. mentella* predominated in the 240–495 m depth range. In the shallow zone, 19 out of 25 sets (76%) had *S. fasciatus; S. mentella* was caught on five sets (20%), and one set (4%) had a possible mixture of redfish species. Below 239 m, 2 out of 68 sets (3%) caught *S. fasciatus*, while the rest of the sets captured *S. mentella* (97%). The latter species was captured on one set as shallow as 172 m, while there was one set where *S. fasciatus* was captured as deep as 262 m.

AFC agreement between surveys

The AFC frequency data (Table 12) for *S. fasciatus* from the winter (79% ≤7, $N = 625$) and summer (76% ≤7, $N = 127$) surveys were very similar for sets with a predominance of the low-mobility A^2 pattern. *Sebastes mentella*, taken from sets identified with a predominance of the high-mobility A^1 pattern, had the following AFC frequencies: 88% ≥8 ($N = 450$) on the winter survey and 91% ≥8 ($N = 249$) on the summer survey. About two times more beaked redfish (687) had AFCs determined on the summer survey than were tested biochemically (376). The AFC frequencies for the entire summer sample (Table 9), for sets considered to represent *S. fasciatus* (77% ≤7, $N = 269$) and for sets considered to represent *S. mentella* (91% ≥8, $N = 418$), were similar to the findings with matching AFC and biochemical data discussed above (Table 12).

Part IV. Comparisons between Areas

AFCs

There was a greater degree of overlap in AFCs between the two beaked redfish species in the Gulf compared with overlaps

TABLE 8. Relative frequency of main EGM passages and TTV insertions from main and small muscles adjusted for polymorphism.

Set No.	No. of fish	No. of EGM branches	% EGM rib passages between ventral ribs: 1–2	2–3	3–4	4–5	No. of tendons	% tendon insertions to vertebral parapophyse: 5	6	7	8	9	10	11	12
Redfish assigned to S. fasciatus															
36	15	16			94	6	54		4	9	28	26	24	9	
28	15	16			94	6	59		5	22	25	24	22	2	
48	15	18		6	61	33	63		10	22	24	14	25	5	
40	14	14		7	93		48	2	6	21	17	23	29	2	
42	15	15			93	7	57	2	2	23	26	25	23		
4	20	22		23	50	27	76		7	20	25	25	20	4	
15	15	22			73	27	52			13	27	31	27	2	
Total	109	123		6	77	17	409	1	5	19	25	24	24	3	
Redfish assigned to S. mentella															
26	11	12		58	42		42		12	24	26	21	17		
41	12	13		38	62		33		9	30	33	24	3		
25	15	15		73	27		59		14	25	25	25	10		
47	4	5		40	60		14			29	29	29	14		
32	4	4		50	50		16			25	25	25	25		
46	12	18		33	67		28			43	43	11	4		
44	14	17		41	53	6	37			32	38	27	3		
11	15	19		53	42	5	36		11	39	42	8			
9	23	24		50	50		51		2	35	45	16	2		
6	8	9		44	56		30		13	23	27	27	10		
17	13	14		57	43		52	2	10	25	25	23	15		
1	4	4		25	75		8			38	50	12			
Total	135	154		49	50	1	406	0*	7	30	33	21	8		

*Zero indicates observations with relative frequency <0.5.

described by Ni (1981b) on NE Grand Bank (Table 12). The relative frequencies of AFCs ≤7 and ≥8 between the Gulf and NE Grand Bank showed, on the average, that 24% of Gulf *S. fasciatus* had AFCs ≥8, compared with 2% from NE Grand Bank. Similarly, 12% of Gulf *S. mentella* had AFCs ≤7 in comparison with 0% noted from NE Grand Bank.

EGM and TTV patterns

The EGM and TTV patterns in the Gulf (Table 13) differ from NE Grand Bank (Ni 1981a) in showing more overlap of main EGM passages (Fig. 7) and in indicating a wider range of the modes and more overlap of the modal TTV insertions for each redfish species. The modes for the TTV insertions ranged from 7 to 10 for *S. fasciatus* and from 7 to 9 for *S. mentella* from the Gulf. Both species had the highest frequency of TTV insertions at 8. Ni found a range in the modes of the TTV insertions for NE Grand Bank *S. fasciatus* from 8 to 10, with the most frequent insertion at 9. For *S. mentella* there was a well-defined mode at 7. Ni did not include the insertion of minor tendons from small muscles in his calculations of the total TTV insertions by species. However, the modes did not change when these were included in the totals in order to make the comparisons.

Statistical comparisons on the raw data (Table 14) within species between sets in the Gulf indicated that the frequency distributions for EGM passages and for TTV insertions (Table 8), respectively, were not significantly different ($P > 0.05$) using the Kruskal–Wallis test. Wilcoxon comparisons (Table 14) within species between the Gulf and NE Grand Bank (Ni 1981a) indicated that the differences in EGM passage patterns were not significant for *S. fasciatus*, but were significant for *S. mentella* ($P < 0.0001$). TTV insertions within species between the two areas were significantly different for *S. fasciatus* ($P < 0.0018$) and for *S. mentella* ($P < 0.0001$). Comparisons within areas in the Gulf and on NE Grand Bank indicated that differences between the two species of EGM passages and of TTV insertions were significant ($P < 0.0001$).

MDH phenotypes

A comparison of the relative frequencies of the three MDH-A phenotypic patterns between the Gulf and St. Pierre Bank showed that the frequencies for *S. fasciatus* were similar (Table 15). However, the frequency for the A^2 pattern (89.8%) was 10% higher in the Gulf than noted for St. Pierre Bank. In the Gulf, 71.3% of *S. mentella* exhibited the A^1 pattern, compared with 100% from Hamilton Bank determined by Payne and Ni (1982). The A^1/A^2 pattern was found with 26.2% of Gulf *S. mentella* but was absent for the specimens of the same species which came from Hamilton Bank and St. Pierre Bank.

Allele frequencies

The pooled allele frequencies of Gulf *S. fasciatus* were compared with those from St. Pierre Bank (Table 16). While some differences were apparent, the *A**2 allele frequency for St. Pierre Bank fell within the range of calculated values for the Gulf (Table 4). *Sebastes mentella* from Hamilton Bank, having only the *A**1 allele, differed from those in the Gulf which had both *A**1 and *A**2 alleles (Table 16).

Discussion

In the present study, we analyzed liver and muscle samples using starch-gel electrophoresis with a slightly acidic amine

TABLE 9. Redfish AFCs compared with biochemistry from the winter survey. F = *S. fasciatus*, M = *S. mentella*.

Mean depth (m)	Set No.	No. of fish for AFC	No. of fish for MDH	% AFCs		% MDH		Species allocation	
				≤7	≥8	A^2	A^1+A^1/A^2	F	M
132	22	48	48	90	10	100	0	100	0
160	174	50	50	64	36	82	18	100	0
162	173	35[a]	35	83	17	100	0	100	0
196	56	50	50	80	20	100	0	100	0
208	163	50	50	66	34	96	4	100	0
236	140	48[b]	48	71	29	81	19	100	0
236	153	47	47	66	34	100	0	100	0
243	36	54	54	93	7	93	7	100	0
243	88	48	48	79	21	75	25	100	0
247	31	49	49	96	4	86	14	100	0
276	95	50	50	88	12	98	2	100	0
285	13	50	50	62	38	80	20	100	0
315	165	46	46	85	15	78	22	100	0
320	184	50	50	38	62	52	48	50	50
355	177	61	61	11	89	1	99	0	100
364	169	49	49	8	92	4	96	0	100
371	176	50	50	12	88	4	96	0	100
395	18	50	50	10	90	0	100	0	100
422	130	50	50	12	88	4	96	0	100
427	164	49	49	6	94	2	98	0	100
440	10	50	50	34	66	0	100	0	100
443	167	45	45	11	89	7	93	0	100
444	3	46	46	4	96	0	100	0	100
132–315	F sets	625	625	79	21	90	10	100	0
320		50	50	38	62	52	48	50	50
355–444	M sets	450	450	12	88	2	98	0	100
Total		1125	1125						

[a]Excluding 15 *S. norvegicus*.
[b]Excluding two *S. norvegicus*.

citrate buffer (pH 6.9) identical to that used by McGlade et al. (1983). The banding patterns for muscle, found by us (Fig. 2 and 3) and by McGlade et al. (1983), differed from the patterns with liver samples. In consideration of the MDH banding patterns found and the buffer systems used by Payne and Ni (1982), McGlade et al. (1983), Dushchenko (1987), Nedreaas and Naevdal (1989), and in this study, it is likely that the redfish muscle protein band patterns represented a composite of MDH-A and MDH-B phenotypic patterns (Utter et al. 1987). It was possible to interpret the skeletal muscle band patterns of all the above studies as representing MDH-A protein banding furthest from the origin and MDH-B banding closer to the origin of each gel. The differences in protein mobility patterns noted between *S. mentella* or *S. norvegicus* versus *S. fasciatus* or *S. viviparus* were primarily due to the respective predominance of the A^1 or A^2 phenotypic pattern. When a three-banded A^1/A^2 pattern was noted with a liver sample, the matching muscle sample (e.g. fish 1030) was found to have an additional a^1a^2 protein band between the two most anodally displaced bands in the gel, indicative of the heterozygotic pattern (Fig. 3). The 100% agreement in species interpretations, derived from liver and muscle samples from the same individual redfish, was because the same MDH-A phenotypic mobility patterns were being scored with both tissues.

Genetic polymorphism can account for the occurrence of the A^1 pattern at localities on the summer survey, where the predominance of the A^2 pattern indicated the presence of *S. fasciatus* (Table 7). Similarly, the infrequent occurrence of the A^2 pattern with fish on sets where the A^1 pattern predominated is best explained by all the fish being *S. mentella* due to MDH-A polymorphism. All the beaked redfish in the shallow zone (99–248 m), with the exception of sets 26, 52, and 54, can be considered to be *S. fasciatus*. The fish from these latter sets, plus all the redfish in the deep zone (256–480 m), are interpreted to be *S. mentella*.

The reidentification of some specimens because of polymorphism does not change the fact that there was a high proportion of Gulf redfish identified as *S. mentella* using MDH-A high-mobility patterns, which had 3–4 and/or 4–5 EGM passage patterns (Tables 6 and 7). There was an overlap of main EGM patterns between *S. fasciatus* and *S. mentella* which was not reported for these species sampled from NE Grand Bank (Table 13).

EGM Patterns

Kenchington (1983) compared the EGM method of Ni (1981a) with the biochemical procedure of McGlade et al. (1983) for 30 specimens of redfish obtained from the Scotian Shelf. The 13 specimens of *S. mentella* and 17 specimens of *S. fasciatus* identified using MDH mobility patterns were in 100% agreement with species identifications obtained from

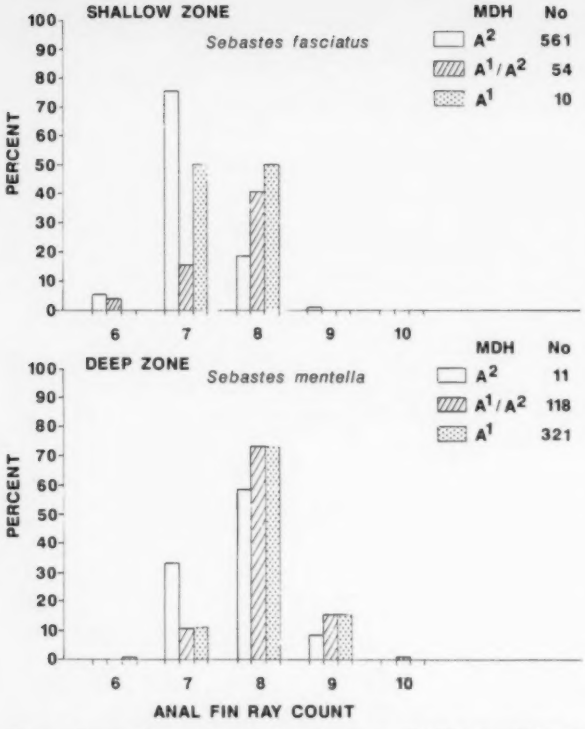

FIG. 4. Comparison of the relative frequency of AFCs in relation to the three MDH-A phenotype patterns for redfish taken from shallow and deep depth zones on the winter survey.

EGM passage patterns. No *S. fasciatus* had a main EGM passing between ribs anterior to the third rib and no *S. mentella* had a main muscle passing posterior to this. There were 197 additional specimens dissected which were not tested biochemically. Eleven fish were identified by Kenchington (1983, appendix 1) as *S. fasciatus*, based on AFCs of 7 and external morphology, but which had the main EGM muscle passing between ribs 2 and 3. There were also 11 unknown redfish labelled *Sebastes*, with AFCs of 8, which had the main EGM passing between ribs 3 and 4. Kenchington questioned whether the EGM route was more variable than Ni (1981a) had suggested, or whether his own interpretation of the EGM patterns was in error.

In the Gulf, it is difficult to explain the high agreement in EGM passage patterns for *S. fasciatus* and the poor agreement for *S. mentella* with the MDH-A mobility patterns (Tables 5, 6, and 7). With *S. mentella* from the Gulf, 47% had Fasciatus group EGM passage patterns (3–4 and/or 4–5). This differed from NE Grand Bank specimens, which all had Mentella group patterns (Ni 1981a). The present contradiction between species identifications, from the biochemistry and from EGM patterns, could cause one to question the accuracy of either data set.

AFC and MDH Patterns

It is conceivable that *S. fasciatus* and *S. mentella* occurred together on some of the sets in the present study. This was true for set 184 on the winter survey (Table 9). The biochemical data, indicating the high prevalence of either the A^2 phenotype or the A^1 pattern on separate sets, strongly suggest that for most sets, *S. fasciatus* and *S. mentella* do not occur together (Tables 7, 9, and 10). The MDH mobility patterns indicate that it is highly probable that all the beaked redfish taken on a set were one species or the other. In the absence of a completely unambiguous method to identify individual beaked redfish to species, it was more reasonable to allocate all individuals on a set to one species than to consider that a second species was present.

On the winter survey (Table 9), *S. fasciatus* was found on all sets at depths from 132 to 315 m and *S. mentella* for all sets at depths 355 to 444 m. On the summer survey (Table 10), the MDH-A mobility patterns indicated the high probability that all beaked redfish at depths from 99 to 248 m, with the exception of three sets, were *S. fasciatus* and that all redfish captured at depths from 256 to 480 m were *S. mentella*.

The MDH mobility patterns agreed with species identifications based on the predominance of AFCs ≤ 7 or ≥ 8 from set to set for two surveys (Tables 9 and 10). They also agree with field identifications based on body colour and external morphological characters (Templeman and Sandeman 1957; Barsukov 1972). Examination of maturities (P. J. Rubec, unpubl. data) during a survey in the Gulf in mid-June 1983 on the *Wilfred Templeman* indicated that >95% of adult (>25 cm total length) female beaked redfish with AFCs, body morphology, and colour patterns characteristic of *S. mentella* had spent ovaries. Adult female redfish with characteristics of *S. fasciatus* had mature ovaries, extruding larvae. The latter predominated at depths <250 m, the former at depths >250 m. This is consistent with the suggestion by Templeman (1980) that *S. mentella* extrudes larvae earlier than *S. fasciatus* and that the two species occupy different depth zones.

Further confirmation that *S. fasciatus* and *S. mentella* usually occur in separate depth zones comes from 9434 vertebral counts obtained from Gulf redfish from 1957 to 1969. Ni (1982) showed that the mean vertebral count at depths <200 m was close to 29.3, while mean counts at depths >200 m were near 30.0 in three statistical areas of the Gulf. Further analysis of these data by D. B. Atkinson (Northwest Atlantic Fisheries Centre, St. John's, Nfld.) found that in December and January, vertebral counts of 29 predominated to depths <300 m and counts of 30 predominated at depths >300 m. In May, October, and November, vertebral counts of 29 predominated at depths <200 m and counts of 30 predominated below 200 m. These data agree with the MDH biochemistry and the AFC data in indicating that the transition depth separating *S. fasciatus* from *S. mentella* is shallower in the spring, summer, and fall than during the winter months.

Associated with the move into deeper water in winter, there is a migration of beaked redfishes towards the mouth of the Gulf off the southwest coast of Newfoundland (Atkinson 1984). This is consistent with winter and summer distribution patterns, respectively, found for *S. fasciatus* and *S. mentella* in the present study (Fig. 5 and 6). However, the winter distribution near the mouth of the Gulf appeared to be more prounounced with *S. mentella* than with *S. fasciatus* (Fig. 5).

60% AFC Rule

For management purposes, on sets where the 60% AFC rule applies in the Gulf, all the beaked redfish could be considered to be one species, either *S. fasciatus* or *S. mentella* (Tables 9 and 10). This interpretation assumed that the phenotypic patterns which disagreed with the dominant pattern were explicable on the basis of MDH-A polymorphism within each species

TABLE 10. Redfish AFCs compared with biochemistry from the summer survey. F = *S. fasciatus*, M = *S. mentella*.

Mean depth (m)	Set No.	No. of fish for AFC	No. of fish for MDH	% AFCs		% MDH		Species allocation	
				≤7	≥8	A^2	A^1+A^1/A^2	F	M
99	20	26	2	85	15	100	0	100	0
170	36	15	15	73	27	100	0	100	0
177	28	43	15	72	28	93	7	100	0
182	48	47	15	72	28	87	13	100	0
183	40	46	15	93	7	100	0	100	0
199	52	40	15	12	88	27	73	0	100
205	42	25	15	84	16	100	0	100	0
213	4	20[a]	20	80	20	100	0	100	0
233	54	25	15	16	84	13	87	0	100
242	30	32	15	63	37	100	0	100	0
246	26	15	15	0	100	0	100	0	100
248	15	15	15	60	40	80	20	100	0
256	41	40	14	10	90	7	93	0	100
273	23	25	15	12	88	0	100	0	100
282	47	30	14	0	100	7	93	0	100
283	25	25	15	16	84	7	93	0	100
285	46	26	15	0	100	0	100	0	100
288	32	33	15	15	85	0	100	0	100
300	44	15	15	0	100	0	100	0	100
304	11	25	15	24	76	13	87	0	100
351	9	25	25	4	96	0	100	0	100
434	3	28	24	4	96	4	96	0	100
464	6	25	17	4	96	0	100	0	100
473	17	15	15	20	80	7	93	0	100
480	1	26	5	4	96	0	100	0	100
99–248		349	172	62	38	74	26	75	25
256–480		338	204	9	91	3	97	0	100
	F sets	269	127	77	23	95	5	100	0
	M sets	418	249	9	91	5	95	0	100
Total		687	376						

[a]Excluding eight *S. norvegicus*.

(Payne and Ni 1982). It was supported by the agreement between the MDH mobility patterns and the AFCs from set to set. All sets with low MDH mobility patterns had a predominance of AFCs ≤7, and all sets with high-mobility patterns had a predominance of AFCs ≥8. For both depth zones, the biochemical results agreed with the species interpretations from AFC data.

Exception to 60% Rule

The 60% AFC rule appeared to work well in most cases. However, situations were encountered on Gulf surveys where AFCs ≤7 or ≥8 were not greater than 60% and a mixture of species was suspected. This was the case with set 33 on the summer survey (Table 11). Most of these redfish designated (?) were juveniles ≤15 cm. Juvenile redfish probably occupy shallower depth zones than adults. Juvenile depth distributions by species are poorly known and should be analyzed separately from those of adult redfish. It is possible that the juvenile redfish with counts ≥8 from set 33 were *S. norvegicus*. In such situations, the violation of the 60% AFC rule on a set would justify a closer morphometric and meristic examination of the redfish during the survey to determine the mix of species present. With juveniles, specimens should be frozen for later biochemical analysis. The biochemical identification of individual redfish to species is currently a two-step procedure, involving separation of *S. fasciatus* from *S. mentella* and *S. norvegicus* using MDH electrophoresis and possibly other isozymes (McGlade et al. 1983; Nedreaas and Naevdal 1989). This should be followed by the separation of *S. mentella* from *S. norvegicus* using isoelectric focusing (Trottier et al. 1989).

Hypotheses to Explain Variation between Sets and Areas

Several hypotheses can be proposed to explain the variation in allele frequencies between sets within species (Table 4) and the greater degree of overlap of AFCs (Table 12) and of EGM and TTV insertion patterns (Table 13) in the Gulf compared with NE Grand Bank: (1) differences in main EGM patterns between *S. mentella* and *S. fasciatus* from the Gulf and NE Grand Bank may have resulted from the limited geographic area sampled in Ni's (1981a) study; (2) geographic differences in AFC and EGM patterns exist due to genetic or environmentally induced differences between populations at various localities; (3) there may be unrecognized redfish taxa present; (4) the variability may be due to the presence of more than one redfish species on trawl sets; (5) the greater degree of overlap in main EGM patterns in the Gulf could have resulted from hybridization between *S. fasciatus* and *S. mentella*.

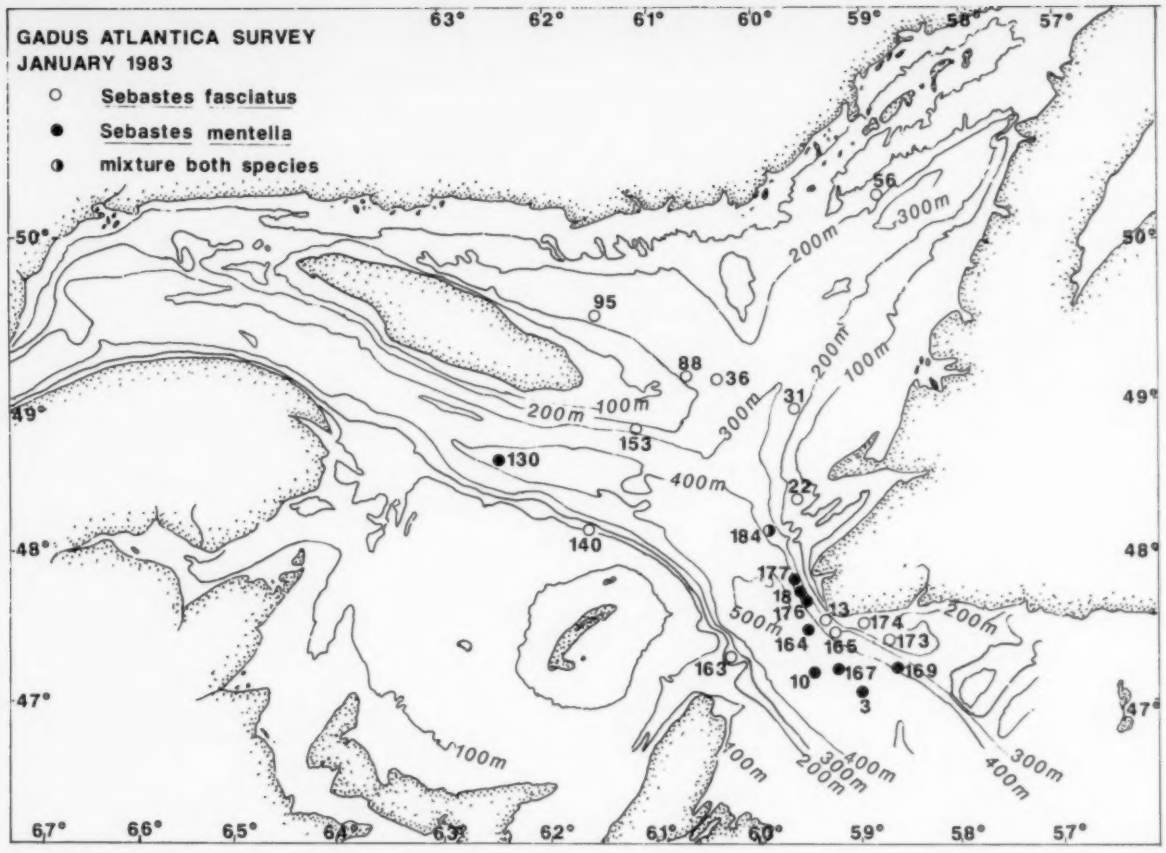

FIG. 5. Distribution of *S. fasciatus* and *S. mentella* during the 1983 winter survey determined from redfish samples with matching MDH biochemistry and AFCs.

(1) The limited number of sampling localities from an area <8 km^2 could have resulted in the low variability of main EGM passage patterns observed with redfish from NE Grand Bank (Ni 1981a). *Sebastes mentella* showed greater variability in EGM patterns in the Gulf, where they were sampled from 16 localities over a wider area (Table 7) in comparison with NE Grand Bank (three sets). But, similar EGM variability was found with *S. fasciatus* from Gulf samples (nine sets) in comparison with the single Grand Bank sample. Hence the differences between the two areas do not appear to be attributable to limitations in sampling.

(2) A genetic mozaic of populations within species of redfish has been proposed by Kenchington (1984). *MDH-A** allele frequency variation (Table 4) might be invoked to support the genetic mozaic hypothesis. *Sebastes fasciatus* and *S. mentella* may have diverged from a common ancestor which had both the *A**1 and *A**2 alleles. Populations within each species would be genetically heterogeneous, with some losing either the *A**1 or the *A**2 allele. At the present, there is little convincing evidence to support this idea.

Altukhov (1974) examined blood group antigen frequencies of beaked redfish sampled along the edge of the Grand Bank. He considered that the differences in length frequencies, sex ratios, and antigen frequencies observed were indicative of localized genetically divergent intraspecific elementary populations. Altukhov did not originally consider that three species, *S. fasciatus*, *S. mentella*, and *S. norvegicus*, were present in the area. He subsequently reexamined his data (Altukhov 1974, 1981) and concluded that 6 of 72 sets were *S. fasciatus* and that the rest were *S. mentella*. No statistics were used to analyze gene frequencies for the antigen data. The differences in antigen frequencies could be due to varied mixtures of the two species, rather than being indicative of intraspecific heterogeneity for genetically diverging populations.

Local aggregations of Pacific ocean perch, *Sebastes alutus*, exhibit different age structures, age–length relationships, length–frequency relationships, ages at maturity, and morphometric variation (Quast 1987; Seeb and Gunderson 1988). Despite this, the species was genetically similar throughout its range, although it did show a gradual genetic differentiation from Washington State to the Bering Sea. The life history characteristics were either influenced by nongenetic factors or were a selective regime not measured by electrophoretic variants.

The nonsignificant differences in the Gulf of main EGM passages and for TTV insertion patterns between sets within each redfish species (Table 14) argue against the genetic mosaic hypothesis of Kenchington (1984). Ni (1982) presented mean meristic data (dorsal ray, anal ray, and vertebral counts) for *S. fasciatus* and for *S. mentella* from different areas off eastern Canada. Although there were minor variations in the mean values between areas, there was no discernable cline of the means for either redfish species. Likewise in the Gulf, there was a

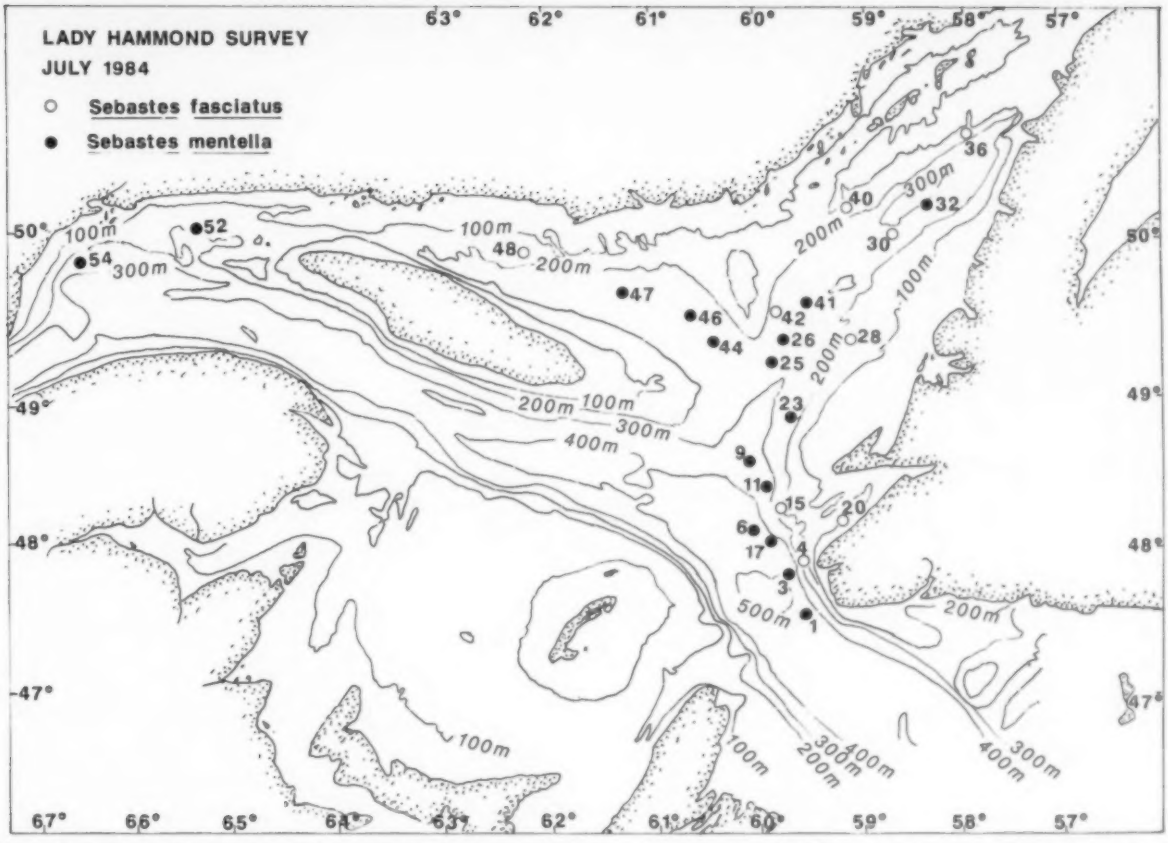

FIG. 6. Distribution of *S. fasciatus* and *S. mentella* during the 1984 summer survey determined from redfish samples with matching MDH biochemistry and AFCs.

lack of significant *MDH-A** genotypic heterogeneity between sets within each species (Table 3). Genetic variation cannot be adequately assessed on the basis of only one allozyme product. However, it is unlikely that genetic divergence or environmental influences can explain the differences observed for AFCs with each species between the Gulf and NE Grand Bank (Table 12), the significant differences of TTV insertions for each species (Table 14), or the significant difference in EGM passages between areas for *S. mentella*.

(3) It is unlikely that additional species of redfish occur in the Gulf over the depth range sampled (99–480 m). Two groups of *S. fasciatus* have been identified, one with both *A*1* and *A*2* alleles at intermediate depths and one usually with only the *A*2* allele at shallower depths (Table 4). At depths <99 m, there have been scattered reports of redfish close to shore in the Gulf. Litvinenko (1979) described *S. fasciatus kellyi* close to shore off Eastport, Maine. Further taxonomic studies of *S. fasciatus* in the Gulf should be conducted to determine whether different subspecies are present.

(4) Heterozygosity per locus values (H_L) and Hardy–Weinberg equilibria were determined in order to test whether more than one beaked redfish species was taken per trawl set. A deficiency of heterozygotes as indicated by negative percent H_L values can occur when there is a mixture of two noninterbreeding populations or species (Campton 1987). A deficiency of heterozygotes can also occur if two species interbreed to a limited extent and the hybrid progeny then mate assortively (introgression) within each parent species. However, a surplus of heterozygotes would be observed if two subspecies or species mated preferentially causing F_1 hybrids to be present in greater number than would occur with random mating. The high H_L value of −26 for set 184 (Table 4) indicated a mixture of two species of about equal proportions. Other negative H_L values from 7 to 12 may be indicative of either some hybridization or the rare occurrence of the opposing species in samples.

Hardy–Weinberg equilibria by set (Table 2) and the nonsignificant heterogeneity G values between sets (Table 3) give genetic evidence that most sets, with the exception of sets 13, 165, 184, and 18, consisted of one species, with *S. fasciatus* predominating in the shallow zone and *S. mentella* in the deep zone. The marked differences noted in allele frequencies by depth zones (Table 4) appear to be due to the fairly discrete depth zones occupied by each beaked redfish species.

(5) Hybridization is the most likely explanation for variation in allele frequencies (Table 4) and the greater overlap in AFCs (Table 12), EGM passage patterns, and TTV insertions in the Gulf compared with NE Grand Bank (Table 13). The MDH mobility patterns (Tables 1, 7, 9, and 10) indicate that *S. fasciatus* and *S. mentella* occupy largely separate depth zones. The summer survey found that *S. mentella* was present in the shallow depth zone for three sets (Table 7). These sets were all made at night, suggesting that *S. mentella* moved up the slope

TABLE 11. Depth distribution of *S. fasciatus* (F) and *S. mentella* (M) determined by AFCs on the summer survey.

Depth range (m)	Species found per set (based on 93 sets)
91–111	
112–129	F, F
130–147	?
148–165	F
166–183	F, F, F, F, F, F, M, F
184–201	M, F, M
202–220	F, F, F, F, F, F
221–239	M, F, M, F
240–256	F, M, M, M, M, M
257–275	M, F, M, M, M, M
276–293	M, M, M, M, M, M, M, M, M, M, M, M, M
294–312	M, M, M, M, M, M
313–330	M, M, M, M, M, M, M
331–348	M, M, M, M, M, M
349–367	M, M, M, M, M
368–385	M, M
386–403	M, M, M, M, M, M, M
404–421	
422–440	M, M, M, M
441–458	M, M
459–476	M, M
477–495	M, M
496–513	
514–530	

TABLE 12. Relative frequencies of AFCs ≤7 and ≥8 in NE Grand Bank and the Gulf of St. Lawrence (matching biochemistry).

Species and area	% AFC ≤7	% AFC ≥8	No. of fish	Study
S. fasciatus				
NE Grand Bank	98	2	100	Ni 1981b
Gulf St. Lawrence	76	24	127	Summer survey
	79	21	625	Winter survey
S. mentella				
NE Grand Bank	0	100	100	Ni 1981b
Gulf St. Lawrence	9	91	249	Summer survey
	12	88	450	Winter survey

into the shallow depth zone at that time of day, possibly associated with a diurnal feeding migration (Steele 1957; Beamish 1966; Atkinson 1989). *Sebastes norvegicus* also occurred in the shallow depth zone. Hence, all three species of Gulf redfish could come in contact facilitating hybridization.

Templeman (1980) examined larval pigment patterns of NW Atlantic redfish species. He proposed that differences in caudal pigment patterns of the larvae of *S. mentella* from the NW Atlantic compared with those from the NE Atlantic may have resulted from hybridization between *S. mentella* and *S. fasciatus* in the NW Atlantic.

Heterozygotes as Hybrids

One can interpret the *A1A1BB** genotype in *S. mentella* and *S. norvegicus* as being indicative of these species and the *A2A2BB** genotype as being characteristic of *S. fasciatus*. Under this interpretation, heterozygotes could be indicative of hybridization between closely related species. The hybridization hypothesis assumes that monomorphic populations of *S. mentella* exist which the only have *A*1* allele. Similarly, monomorphic populations of *S. fasciatus* would have only the *A*2* allele. This idea is supported by the occurrence of pure samples of *S. fasciatus* from sets 22, 56, and 153 on the winter survey and sets 20, 30, 36, 40, and 42 on the summer survey (Tables 9 and 10). No monomorphic sets of *S. mentella* were taken on the winter (Table 1) or summer survey (phenotypic frequencies by set not presented). It is possible that the occurrence of the heterozygotic phenotype (26.2% among *S. mentella*, 8.6% among *S. fasciatus*) and the alternate phenotype (A^2 with the former, A^1 with the latter) resulted from introgressive hybridization between *S. mentella* and *S. fasciatus*.

A sample of *S. mentella*, with only the A^1 phenotypic banding pattern, was taken from Hamilton Bank (Table 15) at a depth of 307–314 m (Payne and Ni 1982). Ni (1982) proposed that *S. mentella* was the predominant redfish species off Labrador based on an analysis of meristic characters. AFC data (22.8% ≤7) led Ni (1982) to suggest that some *S. fasciatus* also occurred at depths <300 m. However, using the 60% AFC rule, these fish would be classified as *S. mentella*. The absence of A^1/A^2 heterozygotes with *S. mentella* from Hamilton Bank (Table 15) may be because *S. fasciatus*, which has the *A*2* allele, was not present to interbreed with the former species. *Sebastes norvegicus* is also present (Power and Ni 1985). However, it is unlikely that heterozygotes would result from hybridization between *S. norvegicus* and *S. mentella* because the *A*2* allele is rare or absent with these species.

Hybridization may be the result of movement of *S. mentella* into the shallow zone. Some populations of *S. fasciatus* being at more shallow depths, have less chance of coming in contact with *S. mentella*. This could explain the occurrence of two groups of *S. fasciatus*, those with and those without heterozygotes (Table 4). The perpetuation of hybrid characteristics among each parent species population, by hybrids which are assumed to be fertile, would explain the prevalence of heterozygotes among both *S. fasciatus* and *S. mentella*.

To further test the hybridization hypothesis, the variation of MDH and other allozyme products should be examined in areas where only one of either beaked redfish species exists. Nedreaas and Naevdal (1989) found that *S. norvegicus* and *S. viviparus* off Norway did not exhibit MDH-A heterozygotic banding patterns. This lends further support to the idea that monomorphic populations within redfish species exist that only have the *A1A1** genotype (*S. mentella* or *S. norvegicus*) or only have the *A2A2** genotype (*S. fasciatus* or *S. viviparus*). Further genetic studies are needed with Atlantic redfishes to verify these ideas.

Of the hypotheses presented, introgressive hybridization between *S. mentella* and *S. fasciatus* in the Gulf appears to be the most likely to explain the phenotypic variations from set to set (Table 1) and the calculated *MDH-A** genotypic frequencies in Table 2. It is also the most likely explanation for the greater degree of overlap of AFCs (Table 12), TTVs, and EGM passage patterns (Table 13) for these species in the Gulf in comparison with NE Grand Bank. If hybridization is occurring between beaked redfishes in the Gulf, one would expect that morphological and meristic characters would overlap between them. This may help to explain the difficulty in identifying these species on research vessel surveys.

Zimmerman and Richmond (1981) demonstrated extensive MDH variation in red shiners, *Notropis lutrensis*. Unlike the

TABLE 13. Comparison of relative frequencies of main EGM passage patterns and tendon insertions by beaked redfish species between NE Grand Bank and the Gulf of St. Lawrence.

Area and no. of fish	No. of EGM passages	% rib passages from main EGM				No. of tendon insertions	% vertebral insertions of tendons from main EGM and small muscles								
		1–2	2–3	3–4	4–5		4	5	6	7	8	9	10	11	12
Sebastes fasciatus															
NE Grand Bank[a] 100	101			94	6	276		0[c]	3	10	21	33	30	1	0
Gulf[b] 109	123		6	77	17	409		1	5	19	25	24	24	3	
Sebastes mentella															
NE Grand Bank[a] 99	105	1	94	5		138	1		11	67	20	1			
Gulf[b] 135	154		49	50	1	406		0	7	30	33	21	8		

[a]Ni (1981a).
[b]Present study.
[c]Observations with relative frequency <0.5.

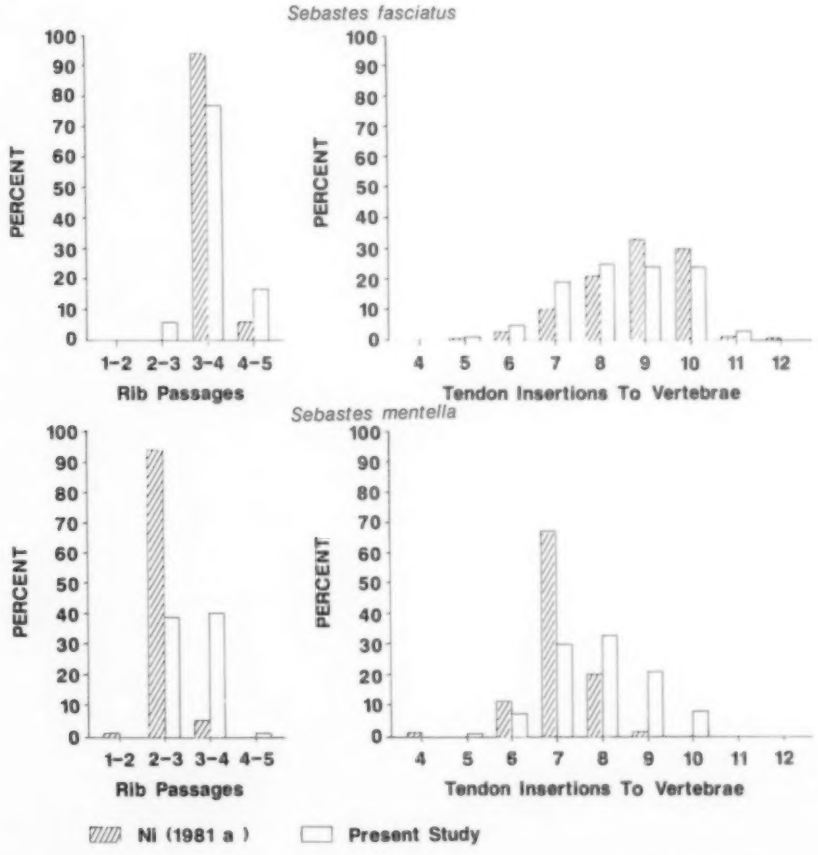

FIG. 7. Comparison of EGM rib passages and TTV insertion patterns for *S. fasciatus* and *S. mentella*, respectively, between the Gulf of St. Lawrence (present study) and NE Grand Bank (Ni 1981a).

TABLE 14. Statistical comparisons of frequency distributions for EGM passages and TTV insertions within and between redfish species.

Species	EGM passages		TTV insertions		Area
	Kruskal–Wallis test within species between sets				
	Prob. > χ^2	df	Prob. > χ^2	df	
S. fasciatus	0.2202	6	0.3189	6	Gulf St. Lawrence[a]
S. mentella	0.6927	11	0.1990	11	Gulf St. Lawrence
	Wilcoxon two-sample test within species between areas				
	Prob. > |Z|	df	Prob. > |Z|	df	
S. fasciatus	0.2330	1	0.0018	1	Gulf St. Lawrence and NE Grand Bank[b]
S. mentella	0.0001	1	0.0001	1	Gulf St. Lawrence and NE Grand Bank
	Wilcoxon two-sample test between species within areas				
	Prob. > |Z|	df	Prob. > |Z|	df	
S. fasciatus and *S. mentella*	0.0001	1	0.0001	1	Gulf St. Lawrence
S. fasciatus and *S. mentella*	0.0001	1	0.0001	1	NE Grand Bank

[a]Present study.
[b]Data from Ni (1981a).

TABLE 15. Comparison of relative frequency of MDH-A phenotypic patterns by beaked redfish species between different areas.

		Phenotype			
Species	No.	A^2	A^1	A^1/A^2	Area
S. fasciatus	625	89.8	1.6	8.6	Gulf St. Lawrence[a]
S. fasciatus	63	79.6	6.8	13.6	St. Pierre Bank[b]
S. mentella	450	2.4	71.3	26.2	Gulf St. Lawrence[a]
S. mentella	31	0.0	100.0	0.0	Hamilton Bank[b]

[a]Present study.
[b]Payne and Ni (1982).

TABLE 16. Comparison of *MDH-A** allele frequencies for redfish from different areas.

	Allele frequency		
Species	*A*2*	*A*1*	Area
S. fasciatus	0.94	0.06	Gulf St. Lawrence[a]
S. fasciatus	0.86	0.14	St. Pierre Bank[b]
S. mentella	0.16	0.84	Gulf St. Lawrence[a]
S. mentella	0.00	1.00	Hamilton Bank[b]

[a]Present study.
[b]Payne and Ni (1982).

present study, most of the polymorphism was with MDH-B. Three alleles combined in different populations of red shiners in the Brazos River, Texas, to exhibit varying degrees of heterozygosity. One of the *MDH-B** alleles is believed to have been transferred to *N. lutrensis* from *N. venustus* through introgressive hybridization. Thermal studies of enzyme activity revealed that MDH-B isozymes of the three allelic forms have different temperature optima (Richmond and Zimmerman 1978). In the Gulf, the differences in allele frequencies at the *MDH-A** locus (Table 4) with *S. fasciatus* and *S. mentella* may be related to the different thermal and pressure regimes usually occupied by these species in separate depth zones. The exchange of alleles through introgressive hybridization between these species may be a beneficial adaptation to fluctuating thermal regimes in the Gulf. It has recently been established that temperature is an important factor influencing catch rates of adult beaked redfish in the Gulf (P. J. Rubec, unpubl. data). Marked changes in bottom temperatures have occurred from 1983 to 1988.

To confirm whether hybridization is occurring, a population genetics study and multivariate analysis of meristic and biochemical characters should be undertaken involving redfish specimens collected from areas with and without suspected hybridization (Campton 1987). Discriminant function analysis (DFA) has been used to separate *S. fasciatus* from *S. mentella* (Ni 1981a; Misra and Ni 1983; Misra 1985; Kenchington 1986a). But, this method has the disadvantage that it requires the a priori classification of individuals into groups being discriminated and that the character used to identify species must be excluded from the DFA. Principal components analysis (PCA) can be used for discrimination studies without making a priori assumptions regarding the classification of individual fish. Kenchington (1986a) also used PCA in an attempt to separate beaked redfish specimens. He concluded that *S. fasciatus* and *S. mentella* were virtually indistinguishable based on PCA analysis using morphological data. With meristic data, the PCA indicated little overlap for two planes between the two species. The papers by Power and Ni (1985), Bailey (1986), and Kenchington (1986a, 1986b) should be consulted before designing a multivariate study concerning hybridization of redfishes.

Buth (1984) noted that hybrids are expected to express intermediate meristic counts compared with the parental species and this intermediacy may apply to other morphological attributes as well. The identification of hybrids becomes difficult if the parentals express similar morphologies, or if there is a substantial difference between the parentals in terms of dominance/recessiveness of the morphological traits. These problems may be minimized by using allozyme characteristics to assess interspecific interactions of hybridization or introgression. Allozymes serve not just as an alternative data base in these comparisons, but may be the data base of choice, since the genetic control of various enzyme systems is known and codominant expression is the rule. Hybrids are often revealed via electrophoresis first on the basis of higher than expected levels of variability and second on the shared, additive nature of their allozyme components with suspected parentals.

Sebastes caurinus and *S. auriculatus* are two Pacific rockfish species that occur sympatrically and appear to segregate by depth. Seeb (1986) conducted analyses on 28 presumptive enzyme loci. The two species were found to maintain separate gene pools in most portions of their ranges. However, at three localities in central and southern Puget sound off Washington State, significant deviations from Hardy–Weinberg expectation were observed at a minimum of two polymorphic loci for every collection. A hybrid index demonstrated that a high proportion of fish in the collections had intermediate values indicative of hybridization.

Restriction endonuclease analysis of mitochondrial deoxyribonucleic acid (mtDNA) is a powerful method (Ferris and Berg 1987; Hallerman and Beckmann 1988) which should be applied to study the population genetics of redfishes. When interspecific hybridization has occurred, one may find the previously diagnostic mtDNA of one form occurring in both species (Avise and Saunders 1984). Hence, mtDNA provides a genetic marker which can act as an indicator of hybridization.

Use of AFCs on Surveys

The present study indicates that using the 60% rule with AFCs allowed beaked redfish to be allocated to species on separate sets on research vessel surveys. AFC data should be collected from a subsample of the redfish measured for length frequencies on each set. This would allow the allocation of length frequencies to the correct beaked redfish species. The collection of otoliths from the same subsample could be used to determine growth and mortality rates by species, in order to estimate the population biomass for each redfish species.

Summary

The present research using MDH biochemistry as a standard indicates that main EGM passages are not a reliable method for separating *S. fasciatus* from *S. mentella* in the Gulf. The time needed to determine EGM patterns also negates their use as a routine field identification method.

This study supports the suggestion of Kenchington (1986a) that electrophoretic techniques are needed for precise identifications and confirms that AFCs can be used to separate beaked redfish species on research vessel surveys in the Gulf. Biochemical methods should be used as a standard with AFCs when evaluating beaked redfish species composition in other geographic areas. AFCs were one of the main characters used to explain beaked redfish species distributions in the NW Atlantic (Ni 1982). The present study provides genetic support for the use of AFCs to identify sets to either *S. fasciatus* or *S. mentella* on surveys. Hybridization is suggested as the most likely explanation for more overlap in EGM passages, TTV insertions, and AFCs between beaked redfish species in the Gulf compared with NE Grand Bank.

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Phenotypic Differentiation in Seasonal Ecotypes of Chum Salmon, *Oncorhynchus keta*

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Tallman, R. F., and M. C. Healey. 1991. Phenotypic differentiation in seasonal ecotypes of chum salmon, *Oncorhynchus keta*. Can. J. Fish. Aquat. Sci. 48: 661–671.

We compared the reproductive environments and phenotypes of early and late season breeding stocks of chum salmon, *Oncorhynchus keta*, to test the hypothesis that seasonal separation has resulted in phenotypically distinct forms. These were autumn- and winter-spawning populations from Bush Creek (Vancouver Island, B.C.) and a winter-spawning stock from nearby Walker Creek. All stocks had a similar time of downstream migration of the fry. No differences were found among the Walker Creek and the autumn-spawning stock of Bush Creek in age at maturity, length composition of spawners, egg size, vertebral counts of adults and fry, and time of fry migration. The winter-spawning stock of Bush Creek differed from the other stocks in egg size and vertebral counts. Discriminant analysis of 10 morphological features of the fry revealed considerable overlap in body form among the stocks. These results do not support the hypothesis that distinct life history morphs are associated with the season of reproduction. We propose that the large amount of similarity in terms of morphology and seasonality among the populations may be the product of selection. Genetic divergence may have occurred to compensate for the environmental differences experienced during embryonic development.

Les auteurs ont comparé les frayères et les phénotypes du saumon kéta *Oncorhynchus keta* de stocks se reproduisant au début et à la fin de la saison, afin de vérifier l'hypothèse que l'écart des saisons entraîne une modification du phénotype. Deux de ces populations, soit des reproducteurs d'automne et des reproducteurs d'hiver, peuplent le ruisseau Bush, tandis qu'une autre population de reproducteurs d'hiver fréquente le ruisseau Walker avoisinant, dans l'île de Vancouver (Colombie-Britannique). Le moment de la dévalaison de tous les alevins de ces différents stocks varie peu. Aucune différence n'a été relevée entre les géniteurs du ruisseau Walker et les géniteurs d'automne du ruisseau Bush pour ce qui est de l'âge à la maturité, la répartition des longueurs des géniteurs, le diamètre des oeufs, le nombre de vertèbres des adultes et des alevins et le moment de la dévalaison des alevins. Par contre, les géniteurs d'hiver du ruisseau Bush se distinguent des autres stocks par le diamètre des oeufs et le nombre de vertèbres. Une analyse discriminante de 10 caractéristiques morphologiques des alevins a révélé un important chevauchement de la forme du corps parmi les stocks. Les résultats obtenus n'étayent pas l'hypothèse que le cycle vital varie selon la saison de reproduction. Selon les auteurs, la forte ressemblance des caractéristiques morphologiques et des fluctuations saisonnières entre les populations peut être le résultat de la sélection naturelle. La divergence génétique peut être apparue en compensation des différences environnementales rencontrées au moment du développement embryonnaire.

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Salmon populations vary phenotypically in space and time (Birman 1981). In chum salmon, *Oncorhynchus keta*, geographically separated stocks vary in many characteristics such as polymorphic enzymes (Okazaki 1981), vertebral number (Kubo 1956), and embryonic development (Smoker 1982, 1986). Temporally distinct stocks, also, vary phenotypically in traits such as time of arrival to the spawning grounds, sexual development, spawning time, distance of migration, length, weight, fecundity, shape, polymorphic enzymes, and karyotype (Berg 1934, 1959; Bakkala 1970; Kulikova 1970; Smirnov 1975; Okazaki 1978; Altukov 1981; Altukov and Salmenkova 1981).

The apparent linkage between phenotypic variation and season of reproduction has led to the hypothesis that, as a consequence of separation in time of reproduction, the morphologic phenotype has evolved in different directions and therefore, "seasonal races" occupy different niches (Ricker 1972; Altukov 1981; Saviatova 1983). This hypothesis has also been stated in the reverse fashion: seasonal differences in spawning time have evolved due to changes in phenotypic characters and in the niche in other periods of the life history (White 1978; Birman 1981). In either case, the general consensus among salmon biologists is that one can identify seasonal races by other parts of the phenotype than the season of spawning.

Correlations observed between spawning season and the morphologic/ontogenic phenotype have been confounded by geographic separation. For example, two distinct morphs, the summer form *O. keta* var. *keta* and the autumn form *O. keta*

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var. *autumnalis*, reproduce in the Amur River, U.S.S.R. However, summer chum salmon spawn in tributaries within 100 km of the mouth of the river, while autumn chum spawn far upstream 1000–2000 km from the sea (Sano 1966). Geographic isolation may be the explanation for the observed differences in phenotype.

Bakkala (1970), Birman (1977, 1981), and Berg (1934, 1959) used environmental data from one system and phenotypic data from another to infer causal links between environment, season of spawning, and phenotype in chum salmon. Beacham (1984, 1987), Beacham and Murray (1986a, 1986b, 1987a, 1987b), and Beacham et al. (1987) compared phenotypic traits of early- and late-migrating segments of different populations on a broad geographic scale without comparing details of the incubation environments. In these studies, no attempt was made to investigate in detail the temporal and spatial distribution of the spawners to discover whether populations were truly temporally isolated or if there were geographic barriers between groups that they sampled.

In temperate ecosystems, populations of poikilotherms reproducing during different seasons experience different thermal environments during incubation. However, stabilizing selection, or selective pressure in the environment for the conservation of form and function of a trait, will encourage genotypes that can compensate for the variance in incubation environment so as to produce the optimum phenotype. Compensatory adaptive responses among allochronic populations will most probably occur in traits with temperature-dependent development. Incubation rate to hatch or emergence (Godin 1982), vertebral number (Tåning 1950; Seymour 1959), and external morphology (Barlow 1961; Fowler 1970) are all known to be related to temperature of incubation. These traits have been correlated with individual fitness in fishes (Riddell and Leggett 1981; Godin 1982; Swain and Lindsey 1984).

In this study, we tested the hypothesis that phenotypic differences observed among seasonal races represent adaptations to the season of reproduction rather than adaptations to geographic location. We compared morphology (vertebral number and external shape) and seasonality (spawning time, length of incubation period, and seasonal time of emergence and downstream migration) between early- and late-spawning populations of chum salmon in the same geographic area. We also compared their incubation environments.

Materials and Methods

Study Area

Bush and Walker creeks are small coastal streams that share the estuary of Ladysmith Harbor (Vancouver Island, B.C.) (Fig. 1). The total streambed available to spawners is approximately 8000 m^2 in Bush Creek and 3000 m^2 in Walker Creek.

According to the Canadian Department of Fisheries and Oceans (DFO, Pacific Biological Station, Nanaimo, B.C.) escapement records from 1950 to 1980, these chum salmon populations have an approximate 2-mo separation in the start, peak, and end of reproduction. Records from 1969 to 1981 were sufficiently detailed to calculate means and 95% confidence intervals for the dates of spawning:

	Start	Peak	End
Bush Creek	Oct. 1: ±3.5	Oct. 28: ±4.5	Nov. 20: ±3.0
Walker Creek	Nov. 16: ±3.5	Dec. 10: ±2.5	Jan. 1: ±4.0

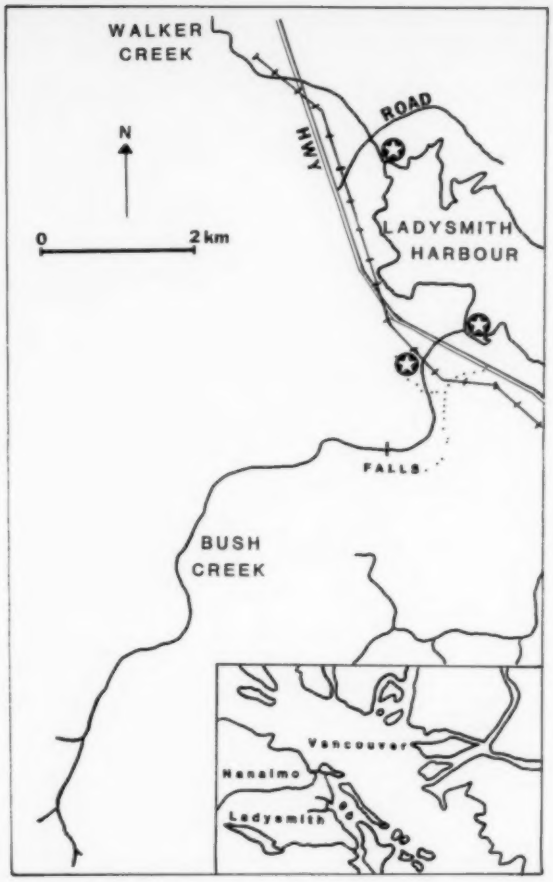

FIG. 1. Bush and Walker creeks of Vancouver Island showing the spawning areas and locations of traps for sampling of fry. Trap locations are marked by a star within a circle. The Autumn Bush stock spawning area lies between the two traps on Bush Creek, the Winter Bush spawning area lies between the upstream trap and the falls, and the Walker stock spawning area is between the trap and the highway on Walker Creek.

These data do not represent full coverage of the potential spawning season. Fisheries officers must apportion their time carefully in order to count spawning numbers in 20–50 streams during the fall. Once the general timing pattern is established the fisheries officers tend to go to a stream to count mainly when they expect to see fish. In this system the sampling of Bush Creek was often discontinued after the third week in November.

Observers counted all spawners in the creeks 3–5 d per week from the beginning of September to February in 1981–82, 1982–83, and 1983–84 to determine the temporal and spatial distribution of spawners. Two temporally distinct spawning populations were observed in Bush Creek (designated "Autumn Bush" (AB) and "Winter Bush" (WB) hereafter), while a winter run was found in Walker Creek (designated "Walker" (W)). The AB population in 1981–82 and 1982–83 was restricted to the lower two thirds of the available spawning area in Bush Creek by a barrier that was impassable until the onsets of freshets in mid-November. Thus, all fish counted below this barrier were classified as AB spawners. All fish observed above the barrier were considered WB spawners. It is important to

note that there was no spatial barrier between the upper and lower spawning areas after mid-November. These circumstances allowed spatial (AB and WB versus W) and temporal (WB and W versus AB) comparisons of phenotypic traits among the three populations (i.e. AB and W are both temporally and spatially separated, WB and W are spatially but not temporally separated, and AB and WB are temporally separated in the same system).

Adult Characteristics

We estimated average age at maturity of the different stocks by reading scale samples from carcasses. The validity of the scale readings was verified by reading otolith age in about 70% of the fish sampled. The European system of recording age (Koo 1962) is used throughout. Chum salmon never have a freshwater annulus. We report the ages without a zero representing freshwater age.

The rapid change of shape due to the development of sexual maturation makes morphometric comparisons of stocks near the date of spawning difficult. However, orbit–hypural length remains relatively constant during the spawning period. Orbit–hypural lengths of carcasses recovered in the steam were measured on each observation day throughout the duration of the runs. The number of adults sampled at each interval was about 10–20% of the total number of spawners present.

Vertebral counts, which remain constant throughout the animal's adult life, were made from adult carcasses of each age and sex recovered in 1982 during the first, second, and third quartiles of the run.

Progeny Characteristics

To determine the timing of the downstream migration of fry, inclined plane traps were set overnight below the spawning areas one to seven times per week from February to July in 1982 and 1983. Once each week the length of time for fry to travel from the spawning area to the trap was estimated by releasing marked fry at the head of the spawning area. Diurnal samples were taken to estimate the proportion of daytime migrants.

Inclined plane traps set at the early-season barrier in Bush Creek were considered to trap only WB progeny. Traps set at estuarine end of the spawning area of Bush Creek would catch both AB and WB progeny. However, given that the AB spawning population was 10–20 times as large as the WB spawning population, we considered the migrating fry caught in these traps to be 90–95% AB progeny.

Downstream migrants were sampled each week for vertebral counts and measurements of external morphology. We analyzed samples at intervals corresponding approximately to the 17th, 33rd, 50th, 67th, and 83rd percentiles of the cumulative frequency distribution of individuals with time in 1982. In 1983, fry were sampled at intervals corresponding approximately to the 25th, 50th, and 75th percentiles of the cumulative frequency distribution. Vertebral counts were made from X-ray photographs. Total length, standard length, head length, eye diameter, snout length, pectoral fin length, body depth, head depth (all to the nearest 0.1 mm), weight (to the nearest 0.1 g), and the number of parr marks were measured for comparison of external morphology.

Rate of Development

Average rate of development for each population may be estimated in the field if one knows (1) when the eggs are spawned and (2) when the fry have completed development. If the temperature during incubation is known, it is possible to compare the time to emergence predicted by temperature-dependent models of development rate and compare it with the actual time to emergence. Chum salmon spawn shortly after entering freshwater in coastal streams, within 30 h of territory formation (Neave 1953; Schroder 1981). Thus, the time of entry is roughly equivalent to the time of egg deposition. The fry migrate to sea after completing embryonic development so time of downstream migration marks the end of embryonic development.

The main environmental variable influencing the rate of development is temperature followed by dissolved oxygen (DO) (Murray 1980; Alderdice and Hourston 1985; Rombough 1988). Incubation environments were compared by measuring water column temperature, intragravel temperature, flow, and DO. Flow, column temperature, and intragravel temperature were measured by spot checks every 1–2 d in 1981. In 1982 and 1983, column temperature was measured by continuous temperature recorders. Intragravel temperature was measured continuously near the recorder and by spot check within redds. Flow measurements were made using the wier method described by Hynes (1976). Water samples were taken from within the redds and DO estimated by standard titration analysis.

We used Murray's (1980) model of the relationship between temperature and incubation rate for chum salmon to standardize comparisons among the populations:

$$(1)\quad E = e^{5.603 - 0.097T}$$

where E is the time to 50% emergence (days) and T is the temperature (constant) of incubation (degrees Celsius).

Murray's model more accurately estimates the speed of development at low temperatures than do others (J. Jensen, DFO, Nanaimo, B.C., pers. comm.); most of embryonic development of progeny from late-spawning adults occurs at low temperatures.

To demonstrate divergence among early- and late-spawning populations, we estimated the number of degree-days required for embryonic development using (1) the time between spawning and fry emergence in each population and (2) the mean temperature of incubation for the entire period of embryonic development. Such an estimate does not account for the seasonally varying temperatures experienced by embryos in nature. To standardize comparisons so that both the thermal regime curve and the curved response to temperature were accounted for, we simulated the effect of the incubation rate – temperature relationship on the daily temperature accumulations using 6°C as a baseline. The adjusted daily thermal units were summed to give an adjusted total accumulated thermal units to emergence for each population. The computations used for a day in which the incubation temperature averaged 10°C are

$$(2)\quad \frac{\mathrm{NT}_j}{6} = \frac{E_{10}}{E_6}$$

where NT_j is the thermal units accumulated during day j and E_i is the predicted emergence time at temperature i and

$$(3)\quad \mathrm{NT}_j = \frac{E_{10}}{E_6} \times 6$$

$$\mathrm{NT}_j = \frac{6 \times e^{5.603 - 0.097 \times 10}}{e^{5.603 - 0.097 \times 6}}$$

Sum of NT_j = the adjusted thermal units (TU's) to emergence.

Egg Size

Egg size is positively correlated with incubation time (Smoker 1986). To determine if egg size difference could account for the differences among the populations in development rate, we measured the moist weight of 100 water-hardened eggs from 30 females from each population in 1982 and 1983.

Statistical Methods

The mode and median were chosen to describe the timing of the adult and fry runs. We used the Peterson mark–recapture method to estimate the proportion of fry captured by our traps. Model 1 or mixed-model two- or three-way ANOVA's were used to analyze differences in phenotypic characteristics among the populations (Sokal and Rohlf 1981). Where sample sizes were unequal, we used standard unbalanced design ANOVA's (Sokal and Rohlf 1981). We considered population to be a fixed effect because we were most interested in the autumn spawning versus winter spawning comparison. We compared means by the Tukey–Kramer procedure to minimize the probability of type 1 error (Sokal and Rohlf 1981).

Stepwise discriminant analysis was used to determine the most important traits for separating the populations. Variables were added into the discriminant function until the multiple correlation coefficient, R^2, of each of the remaining variables with those already entered was greater than 0.40. Mahalanobis distance, D (Mahalanobis 1936), was used to estimate the degree of separation among the populations.

Analysis to test the equality of egg weight on female length regressions among populations was performed using BMDP statistical software program 1R. Population mean egg weights, adjusted for the length covariate, were compared using the GT2 method (Hochberg 1976).

Results

Spawner Characteristics

There was little interannual variation in the timing of spawning in each of AB, WB, and W populations (Fig. 2). AB spawners first arrived during the last week in September, the median date was in the third week of October, and spawning ended by mid-November. AB fish spawned mainly in the lower two thirds of the available spawning area in Bush Creek. WB and W first spawners arrived in mid-November. The median of WB spawner abundance was at the end of November or early December, with most activity finished by mid-December. WB fish spawned mainly in the upper one third of the available spawning area in Bush Creek. The median of W spawner abundance occurred in early to mid-December, with spawning completed by late December or early January.

Temporal overlap among the early and late stocks was slight, with over 95% of the adults of the AB run having spawned and died before 5% of the W and WB spawners arrived. The actual temporal separation may be greater because WB prespawners migrating to the upstream spawning areas or postspawning WB fish drifting back prior to death would have been observed in the downstream area and incorrectly classified as late-spawning AB fish.

Variation in the median day of spawner abundance was much greater among populations than between years. The maximum year-to-year variation of 7 d occurred in W. Year-to-year

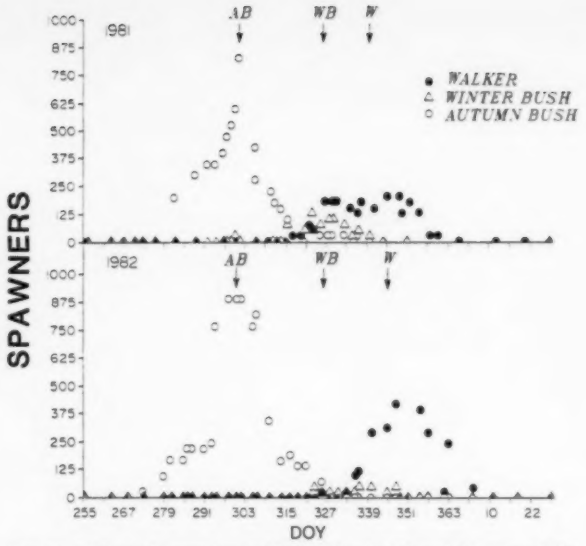

FIG. 2. Timing of spawning in Walker Creek (W) and the upper (Winter Bush (WB)) and lower section (Autumn Bush (AB)) of the spawning area in Bush Creek during 1981 (upper panel) and 1982 (lower panel). Number of live spawners observed versus day number of the year (DOY). Median day of each run shown by an arrow. All spawning areas were observed on each sample day from September 14, 1981, to January 30, 1982, and from September 12, 1982, to January 30, 1983.

variation in AB was 1 d, while there was no year-to-year variation in WB. The variation in the modes was even less, with a maximum difference of 2 d occurring between the 1981 and 1982 WB runs. In contrast, the median of the WB run was 25–26 d later than the median of the AB run in 1981 and 1982. The median of the W was 37–45 d later than the median of the AB run (Fig. 2). The differences among modes of the early stock (AB) and the late stocks (WB and W) were slightly greater than above.

The number of vertebrae differed among populations ($p < 0.05$) but not between sexes or ages (three-way ANOVA years combined). Spatially and temporally separated stocks varied: WB spawners ($\bar{X} = 63.0$) had fewer vertebrae than spatially separated W ($\bar{X} = 65.1$) and temporally separated AB ($\bar{X} = 64.9$) spawners.

Age at return differed among populations for 1982 (two-way ANOVA, df = 2,193, $p < 0.05$, $\bar{X}_{AB} = 2.83$, $\bar{X}_{WB} = 2.39$, $\bar{X}_{W} = 2.59$). No significant differences in treatment or interaction effects were discovered in the 1981 data on age ($N = 431$). Comparisons among means showed that during 1982 the late stocks combined (WB and W) comprised younger spawners ($\bar{X} = 2.52$ yr, $N = 138$) than the early stock (AB) $\bar{X} = 2.83$ yr, $N = 59$) (Table 1). No significant differences in age of return of spawners were found in comparisons where there was a spatial or spatial plus temporal separation among stocks.

O-H length differed among populations and age groups in 1981 ($df_{pop} = 2,418$, $p < 0.05$; $df_{ages} = 1,418$, $p < 0.05$). No significant differences were found due to population, age, or sex or their interactions in the 1982 comparisons. Comparisons among means showed that in 1981, WB spawners were larger ($\bar{X} = 58.52$ cm). than AB spawners ($\bar{X} = 55.75$ cm)

TABLE 1. Age at return for 1981 and 1982 AB, WB, and W spawners. Means, standard deviations, and sample sizes of populations by sex.

		AB			WB			W		
Year	Sex	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N
1981	Female	2.88	0.426	130	2.87	0.344	23	2.72	0.484	65
	Male	2.79	0.490	135	2.88	0.353	8	2.78	0.508	70
	Combined	2.84	0.461	265	2.87	0.341	31	2.76	0.496	135
1982	Female	2.96	0.615	30	2.36	0.487	44	2.65	0.538	37
	Male	2.69	0.541	29	2.45	0.510	20	2.54	0.505	37
	Combined	2.83	0.592	59	2.39	0.492	64	2.59	0.521	74

TABLE 2. Orbit–hypural plate lengths of 1981 and 1982 AB, WB, and W spawners. Means, standard deviations, and sample sizes stratified by population, sex, and age.

			AB			WB			W		
Year	Sex	Age	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N
1981	Female	0.2	51.10	2.639	20	52.00	1.732	3	53.16	2.873	19
	Female	0.3	55.83	6.276	110	58.75	3.998	20	57.37	2.916	46
	Male	0.2	52.19	2.851	31	54.00	0.000	1	55.44	3.110	18
	Male	0.3	57.61	4.029	104	61.29	3.729	7	57.81	8.655	52
	Combined	—	55.75	5.322	265	58.52	4.456	31	56.68	6.029	135
1982	Female	0.2	54.30	2.042	5	53.52	4.143	28	53.56	3.021	14
	Female	0.3	56.03	3.248	25	53.84	5.094	16	54.41	4.497	23
	Male	0.2	54.31	2.964	10	53.84	4.132	11	53.16	4.006	17
	Male	0.3	55.34	3.249	19	55.31	6.198	9	53.85	5.208	20
	Combined	—	55.37	3.100	59	53.90	4.634	64	53.81	4.325	74

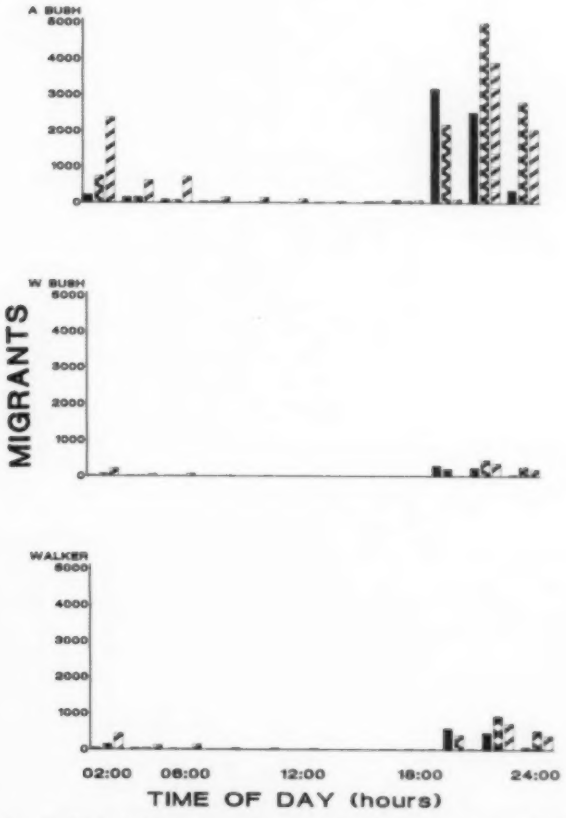

FIG. 3. Diel timing of emergence of fry from the Autumn Bush (A Bush), Winter Bush (W Bush), and Walker stocks.

TABLE 3. Capture efficiency of inclined plane traps below the AB, WB, and W spawning areas during 1983. NM = number marked, NR = number recovered, TC = total catch.

	AB			WB			W		
Date	NM	NR	TC	NM	NR	TC	NM	NR	TC
April 5	25	11	174	0	0	0	50	26	322
April 12	50	21	201	0	0	0	25	10	67
April 19	50	15	1507	25	18	99	50	30	373
April 26	100	36	1588	100	62	797	50	24	236
May 3	100	30	1013	100	51	697	100	53	462
May 14	25	3	322	25	11	248	25	2	107
Total	350	116	4805	250	142	1841	300	145	1567

(Table 2). No significant spatial or spatial and temporal differences among stocks were found.

Progeny Characteristics

In both streams, 95% of the fry migrated at night (Fig. 3). Of marked fry released upstream from the inclined plane traps, 98% of recaptures were made the same night, suggesting that fry complete the journey to the estuary the same night as they emerge from the gravel. Approximately 33% of the AB fry, 48% of the W fry, and 57% of the WB fry migrating downstream were captured by the trap (Table 3).

The year-to-year and interpopulation variations in the timing of the fry run were similar. The average of the difference in the median between years was 7 d and among populations was 9 d. Timing of fry run was reversed among stocks compared with that of the adult populations so that the progeny of stocks that spawned late in the year were the earliest to migrate. Differences in the timing of downstream migration of fry were greater in comparisons among spatially separated stocks than among

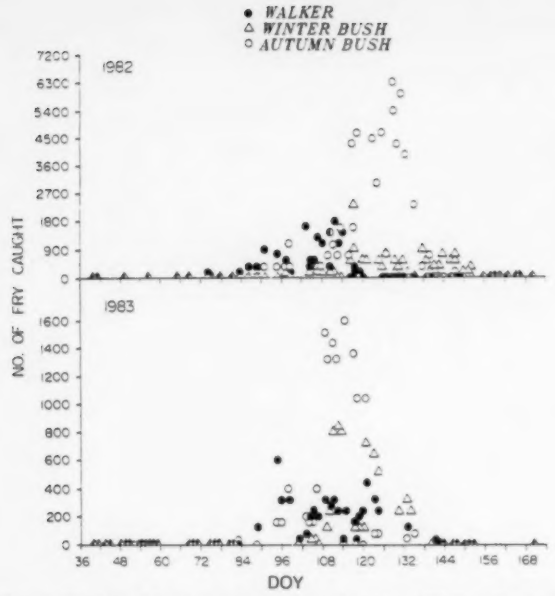

FIG. 4. Timing of fry downstream migrations from Walker Creek and the upper and lower sections of the spawning area in Bush Creek during 1982 (upper panel) and 1983 (lower panel). Number of fry captured in inclined plane traps versus the day number of the year (DOY).

temporally separated stocks. Based on the median dates, the WB fry run was 1–2 d earlier than the AB run in 1982 and 1983 and the W fry run was 5 (1983) and 22 (1982) d earlier than the AB run (Fig. 4).

Vertebral counts in the 1982 fry differed among spatially and temporally separated populations (df = 2,342, $p < 0.05$). WB fry had more vertebrae ($\bar{X} = 67.0$, $N = 120$) than spatially separated W ($\bar{X} = 66.3$, $N = 111$) and temporally separated AB ($\bar{X} = 66.4$, $N = 126$) fry. No significant difference were observed where there was temporal plus spatial separation among populations.

Vertebral counts in the 1983 emerging juveniles also differed among the populations (df = 2,445, $p < 0.05$, $N = 450$). WB fry had fewer vertebrae ($\bar{X} = 64.9$, $N = 150$) than spatially separated W ($\bar{X} = 66.6$, $N = 150$) and temporally separated AB ($\bar{X} = 67.3$, $N = 150$) fry. As well, AB fry had more vertebrae than the spatially and temporally separated fry of W, but the magnitude of the difference was not as great as in the other comparisons.

Year-to-year variation in vertebral count of the juveniles was not significant in W and AB. However, WB juveniles showed substantial year-to-year variation in vertebral count. As a consequence, year-to-year interpopulational divergence of vertebral counts of juveniles was large.

The pooled error variance of the adult vertebral counts was greater than the fry vertebral counts ($VAR_{(adult)} = 5.87$; $VAR_{(juvenile,\ 1982)} = 1.53$; $VAR_{(juvenile,\ 1983)} = 1.17$; Bartlett's test, $p < 0.01$).

The greatest difference in morphology occurred between the W and AB fry in both years (Mahalanobis distance, D, between AB-WB, AB–W, and WB–W = 1.19, 5.72, and 2.68, respectively, for 1982 juveniles and 0.55, 0.91, and 0.69, respectively, for 1983 juveniles). Discriminant analysis of morphometric measurements from emerging fry was moderately successful in discriminating among the AB, WB, and W populations when comparing samples within each year (Table 5), but different characters were important discriminators between years (Table 4). In both years, W fry had fewer parr marks than WB and AB fry ($p < 0.05$) (Table 6). In 1982, AB fry had deeper heads and shorter snouts than WB and W fry whereas in 1983, AB fry had shallower heads than WB fry and WB had longer snouts than W fry ($p < 0.05$). Some characteristics were useful discriminators only in particular years. For example, in 1982, W fry had smaller eyes than WB and AB fry and W fry were lighter than AB fry ($p < 0.05$). In 1983, AB fry had shorter heads than WB and W fry ($p < 0.05$). When classification of the 1983 samples was attempted using an 1982 discriminant function, a large number of misclassifications occurred (Tables 4 and 5); over 40% of WB samples were misclassified.

Rate of Development

Intragravel water in Walker Creek was 0.58° warmer than Bush Creek during the 1981–82 incubation period ($p < 0.001$) and 0.59° warmer than Bush Creek during the 1982–83 incubation period ($p < 0.001$). Water column temperatures in Bush Creek were, on average, 0.91° warmer during the 1982–83 incubation period compared with 1981–82 ($p = 0.021$). Water column temperatures in Walker Creek were, on average, 0.90°

TABLE 4. Variables entered into the 1982 and 1983 discriminant functions for migrating juveniles ranked by importance with classification functions for each. The values under discriminant function represent the coefficients associated with each character under study.

			Discriminant function					
	Ranking		1		2		3	
Variable	1982	1983	1982	1983	1982	1983	1982	1983
Eye diameter	1	—	9.29	—	9.31	—	8.81	—
Snout length	2	4	0.20	−1.05	0.63	−0.83	1.31	−1.12
Weight	3	—	−0.55	—	−0.57	—	−0.58	—
Parr marks	4	1	0.71	5.61	0.79	5.42	0.02	5.02
Head length	5	2	1.12	3.75	1.20	3.94	2.09	3.95
Head depth	6	5	3.33	1.41	3.27	1.66	3.06	1.44
Total length	7	7	2.04	−0.71	2.05	−0.85	2.09	−0.72
Body depth	—	3	—	2.84	—	2.66	—	2.99
Standard length	—	6	—	2.04	—	2.18	—	2.01

TABLE 5. Classification matrices for 1982 and 1983 AB, WB, and W fry samples using the discriminant functions shown in Table 6. The year represents the emigration year.

Year	Group	% correct	Cases classified into group		
			AB	WB	W
1982	AB	64.0	96	46	8
	WB	58.0	28	87	35
	W	81.3	3	25	122
	Total	67.8	127	158	165
1983	AB	52.6	80	30	42
	WB	55.3	40	84	28
	W	61.2	3	36	92
	Total	56.4	142	150	162
1983[a]	AB	3.8	6	54	92
	WB	19.0	6	30	166
	W	66.7	6	44	100
	Total	30.0	18	128	308

[a]1983 classified by discriminant function developed from 1982 data.

warmer during the 1982–83 incubation period than in 1981–82 ($p = 0.002$; Fig. 5). In 1981–82, gravel temperatures taken in the redds were, on average, 0.132° warmer than the column temperatures in Bush Creek ($t = 3.60$, $p < 0.05$). No significant difference was observed between the column and gravel temperatures of Walker Creek in 1982–83.

The temporal pattern of spawning in the creeks results in a marked variation in the temperature regimes experienced by the embryos of the different populations (Fig. 5). For AB embryos, temperature starts out high in October, declines to a minimum in January, and then climbs again to the time of fry emergence. For WB and W embryos, temperature starts out close to the minimum and then climbs to spring values. These differences cause the embryos of early- and late-spawning stocks to experience different temperatures during particular developmental stages.

Progeny of the AB run accumulated more thermal units before emerging than either WB or W progeny (Table 7). All populations appeared to require fewer degree-days to reach emergence in 1982–83 than in 1981–82 (Table 7). In both years the actual incubation time of AB was longer than predicted (Table 7), while actual incubation times of WB and W were shorter than predicted. When degree-days were adjusted to account for variable incubation rates at different temperatures, the year-to-year variation disappeared whereas the variation among stocks remained constant (Table 7).

Regression equations describing the relationship between egg weight and female post-orbit–hypural plate length are as follows:

$$\text{AB: Egg weight} = -0.23808 + 0.00980 \times \text{length} \quad (R^2 = 48.5\%,\ p < 0.001)$$

TABLE 6. Means and standard deviations of morphological characteristics of 1982 and 1983 AB, WB, and W fry samples. SM = means standardized to a common length among samples; WT/TL = weight/total length; KD = Bams (1970) condition index.

Characteristic	1982						1983					
	AB		WB		W		AB		WB		W	
	Mean (SM)	SD	Mean (SM)	SD	Mean (SM)	SD	Mean (SM)	SD	Mean (SM)	SD	Mean (SM)	SD
Head length (mm)	8.09 (8.06)	0.558	8.09 (8.11)	0.411	8.10 (8.11)	0.275	8.11 (8.11)	0.307	8.31 (8.28)	0.358	8.26 (8.28)	0.354
Snout length (mm)	1.22 (1.22)	0.072	1.28 (1.29)	0.135	1.38 (1.38)	0.175	1.49 (1.49)	0.235	1.58 (1.56)	0.228	1.48 (1.48)	0.188
Pectoral fin length (mm)	3.98 (3.98)	0.093	4.02 (4.03)	0.228	4.05 (4.05)	0.220	3.67 (3.67)	0.377	3.79 (3.77)	0.379	3.68 (3.70)	0.407
Eye diameter (mm)	2.97 (2.96)	0.167	2.93 (2.93)	0.174	2.77 (2.77)	0.128	2.95 (2.95)	0.122	2.99 (2.98)	0.085	2.98 (2.99)	0.093
Head depth (mm)	4.91 (4.89)	0.326	4.79 (4.81)	0.263	4.66 (4.67)	0.233	4.43 (4.44)	0.333	4.59 (4.57)	0.274	4.53 (4.54)	0.281
Body depth (mm)	5.12 (5.10)	0.353	4.97 (4.98)	0.253	4.99 (5.01)	0.264	4.88 (4.88)	0.284	4.84 (4.83)	0.247	4.96 (4.97)	0.255
Weight (g)	4.14 (4.06)	0.742	3.67 (3.71)	0.465	3.42 (3.44)	0.375	3.65 (3.66)	0.475	3.69 (3.65)	0.456	3.76 (3.80)	0.446
Parr marks	9.4 (9.3)	1.20	9.5 (9.5)	1.19	8.5 (8.5)	1.16	9.5 (9.5)	1.37	9.3 (9.2)	1.13	8.6 (8.6)	1.09
Trunk length (mm)	28.63 (28.40)	1.373	28.23 (28.35)	1.408	28.23 (28.35)	1.296	23.62 (24.33)	1.051	23.63 (23.49)	01.53	23.36 (23.48)	1.042
WT/TL	1.08 (1.06)	0.16	0.98 (0.98)	0.09	0.91 (0.91)	0.08	0.98 (0.98)	0.10	0.99 (0.98)	0.10	1.01 (1.02	0.09
KD (Bams 1970)	1.94	0.54	1.91	0.45	1.86	0.43	1.92	0.47	1.92	0.46	1.94	0.43

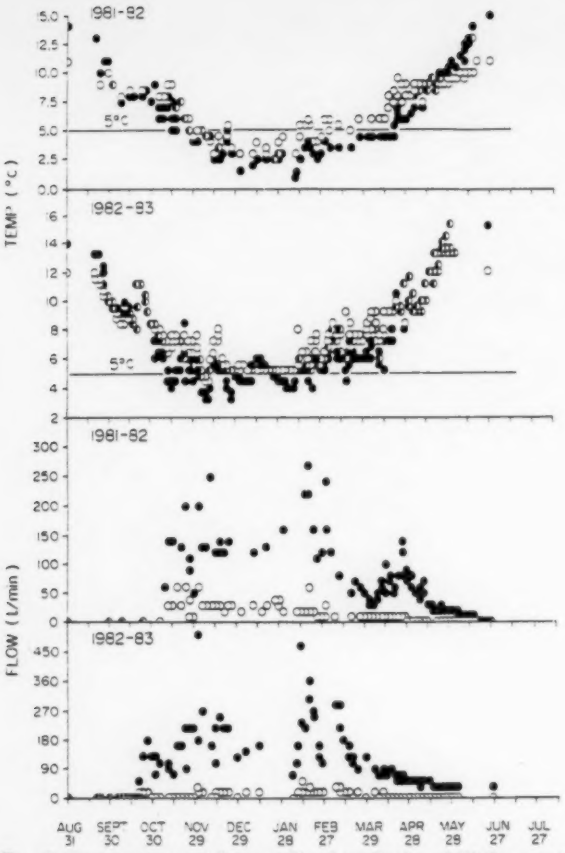

FIG. 5. Temperature and flow profiles from Bush and Walker creeks during 1981–82 and 1982–83. Solid circles = Bush Creek; open circles = Walker Creek.

WB: Egg weight = $-0.19542 + 0.00862 \times$ length
($R^2 = 67.5\%, p < 0.001$)

W: Egg weight = $-0.20122 + 0.00926 \times$ length
($R^2 = 56.4\%, p < 0.001$).

The lines were not equivalent (ANOVA, df = 4,404, $p < 0.00001$): WB was different from AB (df = 2,286, $p < 0.00001$) and W (df = 2,266, $p < 0.00001$ (Fig. 6). The slopes of the W and AB regression lines were equivalent ($F = 2.61$, df = 2,266, $p = 0.07568$) whereas the slopes of the WB and AB regressions of egg weight versus length were significantly different ($F = 8.26$, df = 2,286, $p < 0.001$). The slopes of the WB and W lines were equivalent ($F = 1.78$, df = 2,266, $p = 0.203$) but the adjusted mean egg weight differed ($F = 25.25$, df = 1,197, $p < 0.0001$). Comparisons among adjusted means using GT2 method revealed that WB egg weights ($\bar{X} = 0.26903$) were significantly lower than W ($\bar{X} = 0.29793$). Generally, over the normal range of female size, WB eggs are also smaller than AB eggs (Fig. 6).

Discussion

Despite eggs being deposited during different seasons, the fry of AB, WB, and W emerged from the gravel and migrated in relative synchrony. During the egg to fry phase, the offspring of early- and late-spawning stocks develop under qualitatively and quantitatively differing thermal conditions but, by virtue of their synchronous timing of downstream migration, occupy a common environment during the coastal juvenile phase. The synchronization of migration among the populations appears to be the result of intrinsic incubation rate differences between early and late stocks rather than temperature or other environmental differences between the spawning areas. We found no evidence from our measurements of intragravel temperatures that the late stocks were utilizing sites with warmer temperatures than the values recorded in the water column. It is clear that the late stocks (WB and W) require substantially fewer temperature units to reach emergence than the early stock (AB). In general, we did not see evidence for phenotypic distinctness among seasonally separated stocks. Vertebral count differed among spatially and temporally separated populations but not among populations that were separated by both space and time. Similarly, there was a lack of significant differences in age and size of adults in the two stocks most likely to diverge, W and AB. The same pattern was evident in egg size variation. There was substantial overlap in morphology, with the greatest difference occurring between AB and W progeny.

The hypothesis that a distinctive phenotype is associated with season of reproduction is not supported by our results, least in terms of there being two ecotypes occupying distinct niches throughout their lives. However, the proposed alternative, that phenotypic variation would be associated with spatial separation, was not corroborated by the results either. There was a large amount of similarity in morphology and seasonality in the offspring of the three populations. In the instances where there was phenotypic variation the intermediate population in time and space stood out as being different. A unifying explanation for these results is difficult to achieve. Two alternatives could be plausible: (1) there is a generalized phenotypic optimum for all populations determined by the selective conditions in Ladysmith Harbor or (2) selection acts on each population inde-

TABLE 7. Comparisons of accumulated degree-days (raw and adjusted data) and incubation times (actual and predicted) for AB, WB, and W stocks in 1981–82 and 1982–83 (calculated from median day of adult and fry runs).

	Year	AB	WB	W
Mean temp. of incubation (°C)	1981–82	4.82	3.66	4.36
	1982–83	5.68	5.48	6.45
Total days to emergence	1981–82	192	165	133
	1982–83	180	153	130
Predicted days to emergence	1981–82	182	204	191
	1982–83	168	172	156
Difference (actual − predicted)	1981–82	+10	−39	−58
	1982–83	+12	−19	−26
Accumulated degree-days	1981–82	925.25	603.35	579.65
	1982–83	1022.20	839.20	838.25
Adjusted degree-days[a]	1981–82	1039	845	873
	1982–83	1078	853	834

[a]Degree-days standardized with respect to interannual variations in temperature.

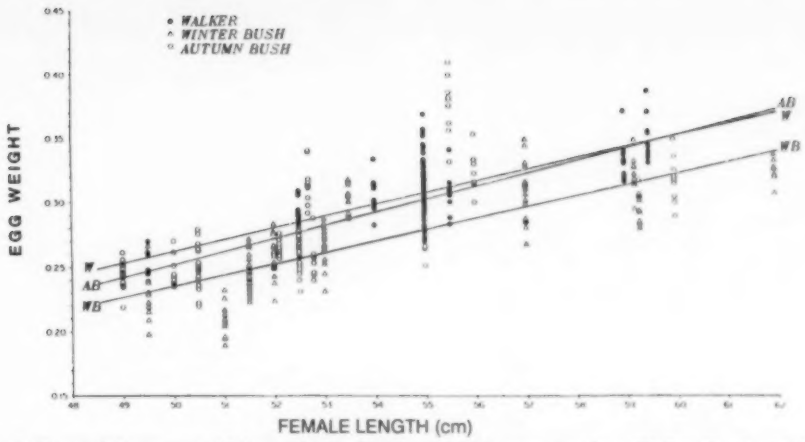

FIG. 6. Egg weight versus orbit-hypural plate length of female spawners from Walker Creek and the upper and lower sections of the spawning area in Bush Creek during 1981 and 1982.

pendently to produce the best phenotype for that group — in some traits the optimum will be the same among the populations, and in others it will not be so.

Stabilizing selection for emergence time and external morphology is clear when one considers the results of Tallman's (1986) experiments with these populations. Tallman (1986) demonstrated that under a common thermal regime the progeny of AB required substantially more time to reach hatch and emergence than the late-spawning stocks. Heritability of time to hatch and time to emergence at 8°C was between 0.35 and 0.5. Independent information provided by Smoker (1982, 1986) also suggested that chum stocks have the capacity to make genetic adjustments in incubation rate. Early and late spawners produced distinctly different morphology (Tallman 1986). The morphological separation between AB and the late stocks in the laboratory was nearly absolute, with only 1% misclassification by discriminant function (Tallman 1986). Our results and Tallman's (1986) taken together show clearly that (1) the phenotype in the wild is canalized relative to that of the laboratory and (2) the canalization is produced by the genotype compensating for the environmental conditions in the field. We conclude that these patterns could only have occurred if stabilizing selection has operated on these traits. The exact agent of this selection we do not know, although other studies of the ecological aspects of synchrony suggest that predation or food limitation may be responsible (Northcote 1978; Peterman and Gatto 1978; Walters et al. 1978; Healey 1979; Sibert 1979; Godin 1982; Miller and Brannon 1982).

The two explanations diverge in their interpretation of the results for other traits where WB appears to be distinct from AB and W. The first would predict that the WB phenotype is maladaptive because it does not conform to the optimum presented by AB and W. This may be reasonable given that WB is the intermediate population in time and space and therefore may not be fully isolated from the AB or the W population. R. F. Tallman and M. C. Healey (unpubl. data) recorded high straying rates of marked individuals into WB. The second explanation would interpret the differences as reflecting a slightly different niche for WB progeny compared with the other two populations. In the case of vertebral number, this seems reasonable because the pattern of intra- and interpopulation variability exhibited in the field was maintained in the laboratory (Tallman 1988). In addition, R. F. Tallman and M. C. Healey (unpubl. data) found with biochemical genetic analysis that gene flow was probably very low among the populations. Strays may not successfully reproduce.

A narrow time window during which the fry of several stocks migrate has been observed in other studies. According to Buklis and Barton (1984), synchrony of fry runs occurs among the summer and autumn chum stocks in the Yukon River. In contrast, at Big Beef Creek on Hood Canal, Washington, early stock progeny emerged 25–30 d before late stock progeny (Koski 1975). However, from spawning to emergence, progeny of the winter stock in Big Beef Creek gained 12–14 d on the autumn stock. Miller and Brannon (1982) provided examples of simultaneous fry migrations among sockeye salmon, *Oncorhynchus nerka*, stocks that spawned during different times of the year.

The evidence for natural selection against asynchronous wild fry is scant. Bilton (1980) showed that the timing of release of hatchery coho salmon smolts could greatly affect survival. Taylor (1980) found that survival of pink salmon fry, *Oncorhynchus gorbuscha*, migrating at the peak time was eight times higher than fry released 33 d earlier. Unfortunately, the fry with lower survival were also considerably smaller than the others at the time of release. Fresh et al. (1982) and Fresh and Schroder (1987) found that individual survival increased with increasing numbers of chum salmon fry released.

We believe that the propensity of ecologists to look for phenotypic differences in nature has prevented investigation of a sizable portion of the genetic variation among populations. Breeding groups isolate themselves from each other by utilizing particular local sites in time and space for reproduction. Their progeny, having gone through embryonic development in different local environments, often mingle in a common selective environment during the nonreproductive phase of their lives. Stabilizing selection will eliminate those genotypes that cannot compensate for the differences among the populations in embryonic incubation environment. Thus, the pressure for phenotypic uniformity will result in genetic change among populations. Ecologists formulate their view of the world by measurement of phenotypes, often without consideration of the underlying processes that have generated those phenotypes (Stearns 1977). Yet, genetic differences among populations

may be manifest by the absence of phenotypic difference rather than its presence.

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Behaviour, Energetics, and Associated Mortality of Young-of-the-Year White Perch (*Morone americana*) and Yellow Perch (*Perca flavescens*) under Simulated Winter Conditions[1]

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Johnson, T. B., and D. O. Evans. 1991. Behaviour, energetics, and associated mortality of young-of-of-year white perch (*Morone americana*) and yellow perch (*Perca flavescens*) under simulated winter conditions. Can. J. Fish. Aquat. Sci. 48: 672–680.

After 150 d of simulated winter conditions, 71.2% of the white perch (*Morone americana*) had died at 2.5°C, while only 11.1% had died at 4.0°C. For yellow perch (*Perca flavescens*), 0.8% had died at 2.5°C, while 17.7% had died at 4.0°C. For both species, small fish died first. Multiple regression models relating overwinter mortality versus fall total length and winter duration predict 3.3 times greater mortality for white perch versus similar sized yellow perch at winter temperature regimes typical of the Great Lakes region. In laboratory tanks, white perch remained active throughout the winter period, while yellow perch sought cover and rested on or near the bottom of the experimental tanks. As a direct consequence, yellow perch had a lower routine metabolic rate and consumed body energy more gradually than white perch. During their inactive wintering period at 4.0°C, yellow perch consumed 25.8% less oxygen than white perch. Actual measurements of dry weight loss indicated that yellow perch in the experimental tanks at 2.5°C consumed 24.6% less dry weight than similar sized white perch. These differences in overwinter behaviour, metabolism, and survival appear to be adequate to account for observed differences in survival of these species in the wild.

Après 150 jours de conditions hivernales simulées, 71,2% des barets placés à 2,5°C étaient morts alors que seulement 11,1% des barets à 4,0°C l'étaient. Quant aux perchaudes à 2,5°C, 0,8% étaient mortes alors que 17,7% de celles à 4°C l'étaient. Chez les deux espèces, c'étaient les poissons de petite taille qui mouraient les premiers. Les modèles de régression multiple qui établissent une relation entre la mortalité au cours de l'hiver et la longueur totale à l'automne ainsi que la durée de l'hiver conduisent à prévoir que, à taille égale et sous des régimes hivernaux de température caractéristiques de la région des Grands Lacs, la mortalité chez le baret est 3,3 fois supérieure à ce qu'elle est chez la perchaude. Le baret placé en bassins au laboratoire est resté actif tout au long de la période hivernale alors que la perchaude cherchait un abri et se reposait au fond des bassins ou tout près. Comme conséquence directe, le métabolisme ordinaire de la perchaude était inférieur à celui du baret qui se trouvait ainsi à dépenser ses réserves énergétiques plus rapidement que la perchaude. Durant sa période hivernale d'inactivité, la perchaude à 4°C consommait 25,8% moins d'oxygène que le baret. Des mesures de la perte en poids sec ont indiqué que des perchaudes des bassins à 2,5°C consommaient 24,6% moins de leurs tissus (en poids sec) que des barets de taille équivalente. Ces différences de survie, de métabolisme et de comportement au cours de l'hiver semblent permettre d'expliquer adéquatement les différences observées de survie chez des sujets à l'état sauvage de ces espèces.

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In the late 1940s the white perch (*Morone americana*) invaded the Laurentian Great Lakes. White perch have since become established in many shallow eutrophic bays throughout Lake Ontario, Lake Erie, and Lake St. Clair and have recently been reported at several locations throughout Lake Huron and in Green Bay, Lake Michigan. An isolated population is also established in Duluth Harbour, Lake Superior. Subsequent to their invasion, fisheries managers throughout the Great Lakes basin postulated potential impacts of white perch on the native fish community. Numerous interactions between white perch and other Great Lakes fishes have been suggested. Prominent among these are competition for food and space with yellow perch (*Perca flavescens*) (Thoits 1958; Christie 1973; Elrod et al. 1981; Owen et al. 1983; Hurley 1986a; Schaeffer and Margraf 1986) and predation on the eggs and/or young of yellow perch and other species (Warner 1974; Elrod et al. 1981; Owen et al. 1983; Schaeffer and Margraf 1987). White perch and native yellow perch appear to have the greatest potential for competition because of their similar size, trophic position, and habitat requirements. Major economic implications are projected for the Great Lakes' commercial fisheries for yellow perch, especially in Lake Erie, should white perch continue to expand their freshwater distribution.

White perch is a schooling species, naturally found in brackish waters along the Atlantic coast of North America as far north as the Miramichi River estuary in New Brunswick. They inhabit shallow warm waters during the summer, but in the fall, white perch migrate to deeper, more thermally stable offshore habitats both in the marine (Thoits 1958) and freshwater (Minns

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and Hurley 1986) environments. Winter feeding activity is reduced (Keast 1968), although adult white perch can be captured by angling through the ice (D. MacLennan, Ontario Ministry of Natural Resources, Tilbury, Ont. N0P 2L0, pers. comm.). Minns and Hurley (1986) noted that white perch are caught throughout the water column during winter in commercial gill nets, indicating that they are active at that time. In contrast, Thoits (1958) described the overwinter behaviour of marine white perch stocks to be in "a state of semi-hibernation."

Yellow perch occur throughout eastern and central North America in small and large lakes as far north as Great Slave Lake and James Bay (Shuter and Post 1990). Both adults and young swim in loose aggregations of 50–200 individuals (Hergenrader and Hasler 1968). The individuals in the schools are close together in the summer, but become more separated in the winter (Hergenrader and Hasler 1968). In Lake Mendota, Wisconsin, a seasonal migration to deeper offshore habitats occurred in the fall (Hergenrader and Hasler 1968). Adult yellow perch also remain active and feed throughout the winter period (Moffett and Hunt 1943; Scott 1955), but, as is the case for white perch, little is known about the behaviour of the young-of-the-year (YOY) in the wild.

Our objective was to compare the winter biology of YOY white perch and yellow perch with reference to overwinter survival and recruitment success. Field evidence indicates that high mortalities of YOY of these species occur during long, cold winters (Hurley 1986b; Post and Evans 1989). Several laboratory and field studies have demonstrated that winter mortality of YOY of several fish species is size dependent, smaller fish suffering higher mortality (Lindroth 1965; Forney 1966; Negonovskaya 1972; Chevalier 1973; Oliver et al. 1979; Toneys and Coble 1979; Shuter et al. 1980; Toneys and Coble 1980; Post 1987; Post and Prankevicius 1987; Henderson et al 1988; Post and Evans 1989; Johnson and Evans 1990). In an earlier study we showed that invasion of white perch into the Great Lakes region was coincident with significant climate warming during the 1940s and that winter survival of YOY is the probable mechanism limiting their freshwater distribution at these latitudes (Johnson and Evans 1990). Climatic factors have been implicated in dominance shifts between associated species (Svardson 1976; Skud 1982). Differential survival of overwintering YOY white perch and yellow perch inhabiting the same lake system could potentially determine their relative success to the extent of causing major shifts in their abundances.

The purpose of this research was to compare the survival of YOY white perch and yellow perch under identical simulated winter conditions in the laboratory, with particular reference to their behaviour and energetics. Our experiments address two main hypotheses: (1) that the native yellow perch is more tolerant to cold winter temperatures than the invading white perch and (2) that differences in winter survival of the two species can be explained by inherent differences in their behaviour and associated energy requirements. The latter hypothesis was tested by observing swimming behaviour in the presence and absence of in-tank cover and by measuring routine oxygen consumption and changes in body mass during winter starvation. Artificial cover was used to test the subhypothesis that behaviour and energy consumption of the two species might be differentially affected by the availability of suitable winter habitat.

Methods

YOY white perch and yellow perch were collected from Lake St. Clair (42°30′N, 82°23′W) during October 1987 and 1988 using a 5-m bottom trawl (1-cm cod end) towed at approximately 0.5 $m \cdot s^{-1}$ for 3–5 min and a 31 × 2.5 m bag seine (6-mm mesh). The two species were transported to the laboratory in separate clear plastic bags containing lake water and an atmosphere of pure oxygen. Temperature was reduced slightly below ambient lake water during transport. At the laboratory the two species were held in separate 535-L tanks at seasonal temperatures until the experiments began (November 29 in both years).

Winter Survival Experiment

Resistance to winter starvation of YOY white perch and yellow perch was tested in 1987–88 and 1988–89. The fish were sorted into twenty-three 2-mm length categories ranging from 54 to 100 mm fall total length. Equal numbers of fish, chosen at random from each length category, were measured to the nearest millimetre and weighed to the nearest 0.01 g and distributed equally among the experimental chambers (79-L insulated wooden tanks coated with nontoxic grey paint, with glass fronts and insulated covers).

In 1987–88, white perch only were tested in duplicate at 4.0°C in the absence of in-tank cover. Their survival was compared with that of yellow perch tested in earlier experiments at 4.0°C by Post and Evans (1989). In 1988–89, winter survival of white perch and yellow perch was tested in duplicate at 2.5°C, in the presence and absence of in-tank cover. The cover consisted of ten 15-cm lengths of 3.8-cm-diameter ABS tubing stacked horizontally in the shape of a pyramid and a 30-cm-long × 10-cm-diameter clay drainage tile.

Experiments consisted of holding the fish without food for 180 d in 1987–88 and 150 d in 1988–89. Natural light and photoperiod corresponding to 44°N latitude was provided. The experimental tanks were supplied with a continuous flow (1.24–1.85 $L \cdot min^{-1} \cdot tank^{-1}$) of nonchlorinated well-water having a pH of 8.09 ± 0.11, conductivity of 474.3 ± 28.8 $\mu mho \cdot cm^{-1}$ at 25°C, and hardness of 244.25 ± 15.00 mg $CaCO_3 \cdot L^{-1}$. Temperatures were maintained at 4.0 ± 0.1°C in 1987–88 and 2.5 ± 0.2°C in 1988–89 and continuously recorded by a Taylor thermograph. Flows and temperatures were also checked at least once daily in each experimental chamber. Dead fish were removed daily and total length, fork length, and wet and dry weights were measured. Fish remaining alive at the end of the experiment (180 or 150 d) were counted and similarly measured and weighed.

Behavioural Observations

In 1988–89, swimming activity and spatial distribution of the fish in the experimental tanks were assessed by direct visual observation and photography. A 5 × 5 cm grid drawn on clear plastic was overlaid in front of the glass windows of the experimental chambers. Activity was quantified by observing the movements of single randomly chosen fish for 5 min and mapping the progressive movements of that fish to successive quadrats. On each occasion, five fish were observed for each species in the presence and absence of cover. Total distance moved per 5-min interval and the direction of movement were recorded. Only fish in the water column were chosen for the swimming activity observations. However, if the fish stopped swimming during the 5-min time interval, as was the case with many of the yellow perch, we continued to record the time (and any progressive movements) until the full 5-min period had elapsed.

Observations were made between 11:00 and 15:00 on days 22, 35, 48, 78, and 112 of the starvation experiment.

Vertical distributions and schooling behaviour of the fish in the experimental chambers were recorded by still photography using low-light film (1000 ASA) under ambient light conditions (without a flash) at three intervals throughout the day (approximately 08:00, 14:00, and 20:00). Observations were made on two occasions during the course of the experiment on days 44 and 65. General observations on swimming activity and distribution of the fish in the tanks were also noted during daily visual inspections of the tanks.

Respiration Experiment

Between March 1 and March 8, 1989 (experimental days 90–97), we measured the routine oxygen consumption of white perch and yellow perch using continuous-flow respirometers (Evans 1972). Three fish of approximately equal size were placed in separate 500-mL sidearm Erlenmeyer flasks and allowed 36 h to recover from handling. The respirometers were housed in circular water baths from which they received an air-saturated water supply at 4.1 ± 0.08°C. Water flow through the respirometers was maintained between 2.3 and 4.0 $L \cdot h^{-1}$ by a siphon and adjusted with a small clamp. The oxygen concentration in the water bath (inflowing water) and outflow from the respirometers was determined for each respirometer once every 15 min, during the 7.5 h of observation, using a polarographic oxygen probe. Oxygen consumed by the fish was adjusted to correspond to a body weight of 4 g by use of a weight exponent of 0.8 (Fry 1971). Energy consumption was calculated by applying an oxycalorific equivalent of 13.6 J·mg oxygen $consumed^{-1}$ (Elliot and Davison 1975).

Energy Loss during Winter Starvation Experiments

Weight loss and loss of condition of all fish in the overwinter starvation experiments were expressed in terms of dry weight. At the start of the experiment, 50 fish of each species, spanning the experimental size distribution, were anaesthetized, killed, measured (fork length and total length), and weighed for live weight. The fish were desiccated at 65°C until the weight stabilized (approximately 48 h) and then were reweighed. At the completion of the experiments, 30 randomly chosen live fish spanning the available size distribution and all of the dead fish from each experimental treatment were similarly desiccated for determination of dry weight. Relationships between dry weight and fork length were then developed for all experimental treatments, both at the start and at the end of the experiment. Weight loss over the course of the experiment was calculated as the difference between the mean individual mass of the fish in a given 1-mm size class at the start of the experiment minus the mean individual mass of the fish in the same size class at the end of the experiment. The regression between dry weight loss and fork length was weighted by the mean number of fish in that size class at the start and at the end of the experiment. The resulting predicted dry weight loss for each size interval was used to estimate energy loss during the experiment.

In order to convert weight loss into the amount of energy utilized, several assumptions were made. Lipid and protein are the principal energy sources during starvation, carbohydrate contribution being minor in comparison (Love 1980). In order to compare energy loss during winter starvation, we assumed that all of the available lipid was utilized before protein was mobilized. Proximate analysis of YOY bluegill sunfish (*Lepomis macrochirus*) and smallmouth bass (*Micropterus dolomieu*) (Savitz 1971; Oliver et al. 1979; Cunningham 1983) revealed the following prewintering percent composition by dry weight: lipid 11–17%, ash 19–21%, and protein 63–70%. Toneys and Coble (1980) indicated that YOY yellow perch from a hatchery in Wisconsin entered the winter with only 6.5% lipid (the lowest value we found in the literature); however, they noted that after 100–120 d of starvation in a laboratory environment, the same fish had a lipid content of 10.6%, suggesting a poor feeding regime in the hatchery (the fish were initially fed when first brought into the laboratory) and/or an unrepresentative sample of fish at the start of their experiments. White et al. (1987) found gizzard shad (*Dorosoma cepedianum*) in Lake Michigan to contain approximately 23% lipid prior to the onset of winter (some of the highest lipid values we found published). No estimates could be found for white perch, but from personal experience, they are a very oily fish, suggesting their lipid levels to be at the higher end of the published range.

In the present study we have assumed lipid and protein to represent 14 and 67% of the fall dry weight, respectively, for both YOY white perch and yellow perch. The total weight loss of starved fish was partitioned by subtracting the fraction of the total body weight comprising lipid (i.e. 14%) as an absolute weight from the observed total weight loss to obtain protein loss. Energy consumed during starvation was then calculated by applying standard equivalents as follows: 1 g of lipid generates 37.91 kJ of energy to the fish, while 1 g of protein yields 20.08 kJ of energy (Brett and Groves 1979).

Results

The mean size of YOY white perch from Lake St. Clair did not differ significantly between the 1987 and 1988 field collections (two-sample t-test: $t = 0.21$, $p > 0.05$, df = 504). Further, the mean size of white perch at the start of the experiments did not differ significantly between 1987 (4.0°C) and 1988 (2.5°C) (two-sample t-test: $t = 0.41$, $p > 0.05$, df = 718) (Table 1). YOY yellow perch collected from Lake St. Clair in the fall of 1988, however, were significantly larger than either year-class of white perch (two-sample t-test: $t = 27.7$, $p < 0.01$, df = 718 for the 1987 white perch; $t = 25.9$, $p < 0.01$, df = 718 for the 1988 white perch) (Table 1). YOY yellow perch collected from Dickie Lake in the fall of 1985 (Post and Evans 1989) were also significantly smaller than either year-class of white perch and the Lake St. Clair yellow perch (two-sample median test (Mood 1950): $\chi^2 = 81.7$, $p < 0.01$ for the 1987 white perch; $\chi^2 = 66.8$, $p < 0.01$ for the 1988 white perch; $\chi^2 = 552.9$, $p < 0.01$ for the 1988 yellow perch) (Table 1).

Winter Survival of White Perch and Yellow Perch

Both species of fish suffered some overwinter mortality in all treatments. After 150 d at 4.0°C, white perch experienced 11.1% mortality, while the smaller size yellow perch suffered 17.7% mortality (Table 1). At 2.5°C, white perch experienced 71.2% mortality, while the larger sized yellow perch suffered only 0.8% mortality (Table 1). The presence of in-tank cover did not affect survival of either species (ANCOVA of probit transformation of cumulative percent mortality over time: $F = 0.39$, $p > 0.05$, df = 18 for white perch).

In earlier experiments, survival of yellow perch at 4.0°C (Post and Evans 1989) and white perch at 2.5 and 4.0°C (Johnson

TABLE 1. Observed and predicted overwinter mortality of starved YOY white perch and yellow perch at 2.5 and 4.0°C. Data for yellow perch at 4.0°C are from Post and Evans (1989), white perch results at 4.0°C are from Johnson and Evans (1990), and results for both species at 2.5°C are from the present study. T_w = mean water temperature.

Species	Conditions of treatment: T_w (°C)	Conditions of treatment: In-tank cover	Actual body size: TL (mm)	Actual body size: Weight (g)	Observed mortality at 150 d (%)	Predicted mortality (%) at 150 d for a fish of TL: 55 mm	70 mm	85 mm	Predictive equation[a]
White perch	2.5	Cover present	71.8	4.18	73.9	100.0	67.7	38.0	$PMORT = 0.42 \cdot e^{0.0211\ WD - 0.0384\ TL}$
		No cover	71.8	4.16	68.4				
	4.0	No cover	72.1	3.94	11.1	56.5	16.4	4.7	$PMORT = 1.71 \cdot e^{0.0229\ WD - 0.0826\ TL}$
Yellow perch	2.5	Cover present	85.3	5.66	1.1	—	—	—	Insufficient mortality to develop equation
		No cover	85.2	5.65	0.6				
	4.0	No cover	55.6	1.27	17.7	38.5	4.9	0.6	$PMORT = 16.71 \cdot e^{0.0235\ WD - 0.1381\ TL}$

[a]PMORT = probability of mortality (%), Wd = winter duration (d), and TL = fall total length (mm).

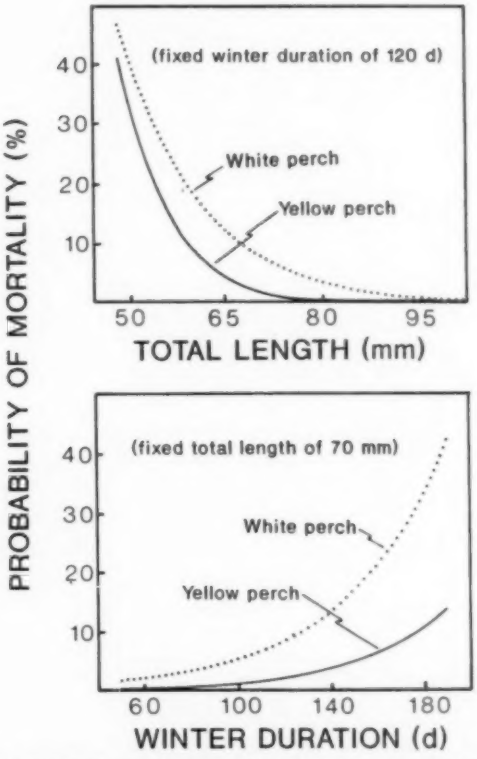

FIG. 1. Predicted overwinter mortality for YOY white perch and yellow perch held at 4.0°C. Comparative plots are for a fish of 70 mm TL and for a winter duration of 120 d. Predicted mortality is based on equations presented in Table 1 developed for white perch at 4.0°C by Johnson and Evans (1990) and for yellow perch at 4.0°C by Post and Evans (1989).

and Evans 1990) was found to be dependent on body size and winter duration. We used multiple regression equations developed in those studies to compare the predicted mortality of the two species under similar winter conditions (Table 1). For white perch and yellow perch of the same body size at 4.0°C and a winter duration of 150 d, the comparison revealed that yellow perch are less prone to overwinter mortality (Table 1). As body size declines, or winter duration increases, the magnitude of the mortality difference between species increases (Fig. 1). Low mortality prevented the development of a predictive equation for the large-bodied yellow perch at 2.5°C; however, the predicted mortality (38%) for similar sized (85 mm total length (TL)) white perch at 2.5°C is well above the observed mortality (1.1%) for yellow perch experiencing the same winter duration (Table 1), again suggesting that yellow perch are better able to survive winter conditions.

Winter Behaviour

White perch were significantly more active than yellow perch held under identical simulated winter conditions. Random swimming speed of YOY white perch averaged 5.18 body lengths·min^{-1} (approximately 0.62 cm·s^{-1}), while the larger yellow perch averaged only 0.68 body lengths·min^{-1} (approximately 0.10 cm·s^{-1}) (Fig. 2). The presence of in-tank cover did not have any significant effect on the swimming performance of the two species (paired t-test: $t = 0.34$, $p = 0.74$, $n = 25$ for white perch; $t = 0.06$, $p = 0.95$, $n = 24$ for yellow perch).

Most of the observed difference in swimming speed can be accounted for by the fact that the yellow perch were not actively moving and remained on or close to the bottom of the tank, either seeking refuge in the cover provided or forming dense stationary schools on the bottom of the tank when cover was not available (Fig. 3). Over 95% of the yellow perch were found in the bottom 10 cm of the tank at all times, with fewer than 10% of the fish swimming at any one time. Where cover was provided, 65–86% of the yellow perch were found within the tubes, with never more than 5% of the fish further than 5 cm from cover. Significantly more yellow perch were found in cover during the midday observations than in either the morning or evening time periods, but at all times the majority of fish utilized cover (Table 2).

White perch, in contrast, remained in the water column during the entire experimental duration and failed to make use of the cover at any time (Fig. 3; Table 2). Zero to 8% of the white perch were found in the top 5 cm of the tank, 3–19% in the next 5-cm depth stratum, 19–25% in the middle 5 cm, 29–35% in the 15- to 20-cm stratum, and 18–43% within 5 cm of the bottom of the tank (Fig. 3). Significantly more white perch were found in the 5- to 10-cm stratum in the presence (16%)

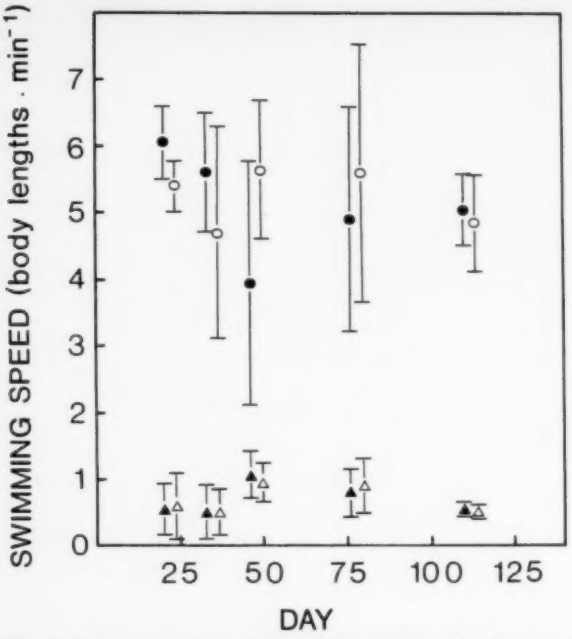

FIG. 2. Swimming activity for YOY white perch and yellow perch held in the laboratory at 2.5°C during the course of the 1988–89 winter experiments. Each symbol indicates the mean of five fish ± 1 SD. Each fish was individually observed over a 5-min period. Circles represent white perch and triangles represent yellow perch. Open and closed symbols represent experiments without and with in-tank cover, respectively.

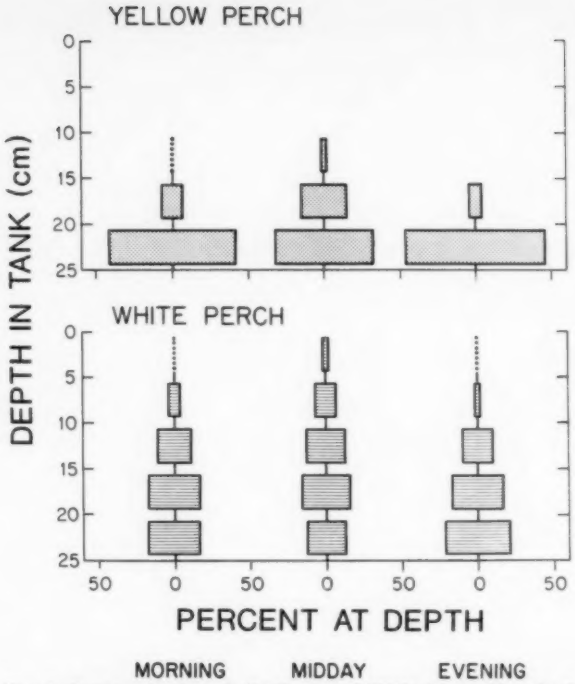

FIG. 3. Comparative in-tank distribution of YOY white perch and yellow perch held at 2.5°C in the absence of in-tank cover. The relative width of each section of each distribution represents the percentage of the total number of fish in the tank found in that depth stratum at that time of day. The holding tanks were 25 cm deep.

versus absence of cover (9%), the cover being approximately 15 cm high. During the day, significantly more white perch were found in the top 5 cm of the water column whereas at night, significantly more were found in the bottom 5 cm, irrespective of in-tank cover. No white perch were ever observed to occupy the tubes, although the occasional fish was observed to swim through the larger clay tile (Table 2).

Bioenergetic Considerations

Routine metabolic rates of unfed white perch and yellow perch at approximately 4.1°C during midwinter were 49.4 and 39.3 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$, respectively, at a body weight of 4 g (Table 3). Incorporating body weight as a covariate, these rates of oxygen consumption are significantly different (ANCOVA: $F = 0.16$, $p > 0.05$, df = 68). Expressing these rates of oxygen consumption in terms of energy expenditure, a 4-g YOY white perch would require 64.5 $J \cdot d^{-1}$ to meet its metabolic demands, while the same size yellow perch would require only 51.3 $J \cdot d^{-1}$. In other words, the routine metabolic rate of YOY white perch is, on average, 25.8% higher than for similar sized yellow perch (ANOVA: $F = 22.10$, $p < 0.01$, df = 68).

On average, surviving white perch lost 27.7 and 36.5% of their initial dry weight at 2.5 and 4.0°C, respectively (range = 19.8–41.7) (Fig. 4A and 4B). No significant relationship was found for the weighted (n = number of fish in the sample) regressions between dry weight loss and body size, although negative slopes were found in each case (Fig. 4). Surviving yellow perch, on average, lost only 19.7% of their initial dry weight (range = 12.7–26.6) when held at 2.5°C (Fig. 4C).

TABLE 2. Mean percentage of YOY white perch and yellow perch using the in-tank cover during simulated overwinter experiments at 2.5°C. The in-tank cover included stacks of 3.8-cm diameter plastic ABS tubing and a 10-cm-diameter clay drainage tile. Photographic observations were used to determine distributions on days 44 and 65 of the overwinter starvation experiment.

Species	Time period	Number of photographs analyzed	Percent of fish in cover	
			Mean	SD
White perch	Morning (08:00)	3	0.00	0.00
	Midday (14:00)	4	0.00	0.00
	Evening (20:00)	3	0.00	0.00
	Combined	10	0.00	0.00
Yellow perch	Morning (08:00)	3	70.74	4.63
	Mid-day (14:00)	4	81.94	3.99
	Evening (20:00)	3	68.89	3.85
	Combined	10	74.67	7.29

Again, no significant relationship was found between dry weight loss and body size. No dry weight measurements were made on the yellow perch at 4.0°C by Post and Evans (1989); however; similar wet weight losses of 25–30% were observed for yellow perch in both studies. Presence of in-tank cover had no effect on weight loss for either species at 2.5°C (ANOVA: $F = 0.13$, $p = 0.72$, df = 26 for white perch; $F = 0.02$, $p = 0.89$, df = 38 for yellow perch). After 150 d at 2.5°C, surviving white perch had lost 24.6% more dry weight than yellow

TABLE 3. Mean weight, oxygen consumption, and weight-corrected oxygen consumption (±1 SD) adjusted to correspond to a 4-g fish for YOY white perch and yellow perch. All fish were observed for a total of 7.5 h on two days approximately 18 h apart. Each determination is the combined result of three fish per respirometer.

Species	Water temperature (°C)	Mean body weight (g)	Mean oxygen consumption ($mg \cdot h^{-1} \cdot fish^{-1}$)	Weight-corrected oxygen consumption ($mg \cdot kg^{-1} \cdot h^{-1}$)	
				Mean	SD
White perch	4.07	1.99	0.115	50.10	7.99
	4.14	3.38	0.183	52.21	13.86
	4.05	4.61	0.201	44.81	5.34
	4.09	6.45	0.296	50.53	9.78
Mean				49.41	9.78
Yellow perch	4.14	2.80	0.118	39.09	6.46
	4.08	4.47	0.165	37.82	9.29
	4.12	5.68	0.217	40.98	7.20
Mean				39.30	7.58

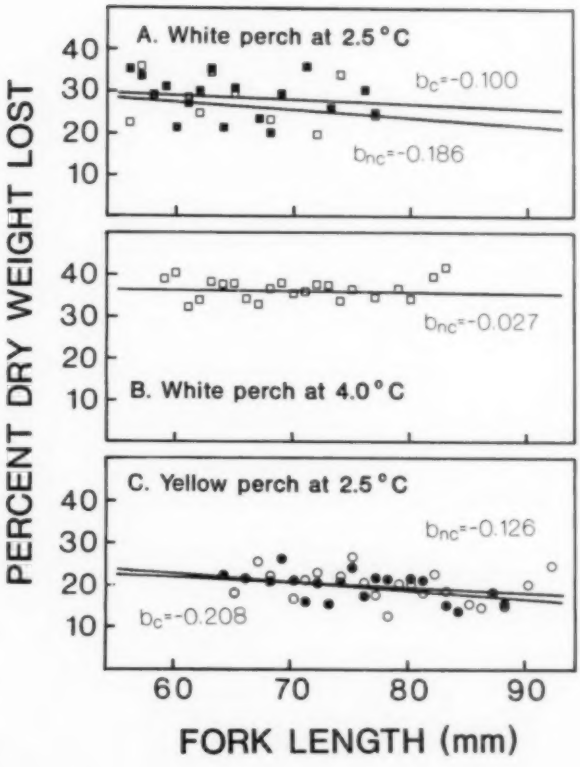

FIG. 4. Proportional dry weight loss versus fork length for surviving white perch and yellow perch at the end of the overwinter experiments. (A) Weight loss for YOY white perch held in the presence and absence of artificial cover at 2.5°C for 150 d; (B) weight loss for YOY white perch held in the absence of artificial cover at 4.0°C for 180 d; (C) weight loss for YOY yellow perch held in the presence and absence of artificial cover at 2.5°C for 150 d. Solid symbols represent fish in tanks lacking cover and open symbols represent fish in tanks containing in-tank cover. The symbols b_c and b_{nc} refer to the slopes of the regressions in the presence of cover and absence of cover, respectively.

perch of the same initial weight (ANOVA: $F = 5.83$, $p < 0.05$, df = 24).

The observed weight loss for an average-sized YOY white perch (72 mm TL, 4.18 g) held at 4.0°C was equivalent to 8.07 kJ of energy by the time the fish died (average time to death = 151 d), or 53.46 $J \cdot d^{-1}$. This calculated energy loss at 4.0°C is in agreement with that estimated from the oxygen consumption rates (64.52 $J \cdot d^{-1}$). At 2.5°C, white perch metabolized just over half (4.18 kJ) the amount of body energy of white perch of the same size at 4.0°C. The endurance time at 2.5°C was 21 d less than at 4.0°C (mean time to death at 2.5°C = 130 d).

Discussion

Significant size-related overwinter mortality was observed for YOY white perch held in the laboratory under simulated winter conditions; however, fewer YOY yellow perch died under similar conditions. YOY yellow perch in Lake St. Clair are, on average, significantly larger than white perch. For smaller yellow perch that are more representative of inland stocks, Post and Evans (1989) observed significant size-related overwinter mortality. The overwinter mortality models predict that, within the range of weather conditions in the lower Great Lakes region (120 d at or below 4.0°C), extant size-classes of fasting white perch (60–100 mm fall TL) would be expected to experience between 22.9 (at 4.0°C) and 40.3% (at 2.5°C) overwinter mortality. Similar sized yellow perch would be expected to experience only 2.2% overwinter mortality at 4.0°C. The yellow perch at 2.5°C were significantly larger than those used by Post and Evans (1989), which explains why no overwinter mortality was observed.

The comparison of white perch and yellow perch from Lake St. Clair at 2.5°C revealed differences in survival that are consistent with the size-corrected differences between Dickie Lake yellow perch and Lake St. Clair white perch at 4.0°C, suggesting that the latter difference is actually a species difference rather than a stock difference due to comparison of stocks of two species from different locations. This is further supported by a study of geographic variation in thermal tolerances within 11 species of North American temperate fishes (Hart 1952) in which was found little evidence of stock differences from

Ontario, Ohio, Tennessee, and Florida. In Hart's (1952) study, phenotypic differences attributable to thermal acclimation and body size, both of which were controlled in our experiments, did have significant effects on thermal tolerances of stocks within species. From this we suggest that local adaptation probably had only minor, if any, effects on the differences observed between yellow perch from Dickie Lake versus white perch from Lake St. Clair. Similarly, although the Lake St. Clair white perch were collected and tested in two separate years, the source of the fish was the same, and no significant differences existed between years with respect to length, weight, or length–weight regressions. Therefore the possibility that the significant difference in overwinter survival may be due to differences in percent lipid and/or protein seems unlikely.

Field studies have identified substantial total mortality of yellow perch during the winter and indicate that survival is higher for cohorts that attain a larger body size by the end of their first growing season. In Oneida Lake, New York, total mortality of 11 cohorts of YOY yellow perch ranged from 72 to 99% between October 1 and May 11 of the following year (Nielsen 1980). Although Nielsen (1980) attributed mortality of juvenile yellow perch during the growing season to predation by walleye (*Stizostedion vitreum vitreum*), overwinter mortality of YOY yellow perch was not positively correlated with walleye biomass (Post and Evans 1989). In Lake St. George, total overwinter mortality in 1984 and 1985 ranged from 42 to 76% for YOY yellow perch 71.4 and 60.7 mm TL, respectively (Post and Evans 1989). Total overwinter mortality has also been measured for wild fingerling brook trout (*Salvelinus fontinalis*), ranging from 27 to 65% during 11 consecutive winters in Lawrence Creek, Wisconsin (Hunt 1969). With both the yellow perch in Lake St. George and the brook trout in Lawrence Creek, mortality was significantly negatively correlated with mean length of the cohort in the fall, and the observed size-related mortality was not due to predation (Hunt 1969; Post and Evans 1989).

For many freshwater fish species including the white perch and yellow perch, winter feeding activity is reduced because temperature is low and food is scarce. During winter, therefore, fish become dependent on stored energy reserves to meet their basal metabolic requirements. In poikilothermic organisms, as the temperature is reduced, so is their metabolic rate (Fry 1971). This affords wintering fish an advantage in that their daily energy requirement is low. In some species of fish, such as the Centrarchidae, activity slows dramatically during winter. The fish seek out cover, remain virtually dormant (Munther 1970), and metabolic rate is depressed (Evans 1984) until day length increases and water temperatures warm in the spring.

Yellow perch in our experiments utilized the in-tank cover where available, or formed small dense aggregations in the corners of the tanks where the cover was unavailable, suggesting a similar adaptation to the centrarchids. Swimming activity virtually ceased, as was observed in a laboratory study by Eriksson (1978), and respiration rates were low, minimizing the utilization of energy reserves. White perch, on the other hand, did not use the in-tank cover and continued to swim throughout the water column. Based on both weight loss and respiration rates, this additional activity by the white perch placed a significantly higher daily demand on their body energy reserves. Ultimately, their energy reserves were utilized more rapidly than those of the yellow perch, and many of the white perch succumbed to starvation.

An alternative explanation for the interspecific differences in overwinter behaviour and survival might be attributable to the experimental procedure, in that white perch may find the habitat unsuitable for overwintering, thereby causing an active searching behaviour and elevated swimming activity compared with the yellow perch. However, habitat preferences for the two species during the remainder of the year (for which information is available) are very similar, and it therefore seems unlikely that differences in overwintering habitat requirements could cause activity to be significantly different, although the possibility cannot be ruled out. Further, while the activity of the white perch might be attributed to foraging behaviour, previous studies have shown that postwintering white perch captured in the field have empty guts (Keast 1968), while YOY white perch held in the laboratory and provided with an excess of food lost a significant proportion of their fall weight (Johnson and Evans 1990). Together these points suggest that, even under natural field conditions, significant overwinter energy loss is likely for white perch.

The quiescent nature of our yellow perch and the more active behaviour of our white perch contest the suggested overwinter behaviour of the species found in the literature. However, most of the literature observations were made on adult fish, and ontogenetic differences might occur with respect to the distribution, activity, and behaviour of adult and juvenile fish (Spooner 1931; Breder and Nigrelli 1935; Coutant 1987). Further, Breder and Nigrelli (1935) have shown that low temperature can induce nonschooling centrarchids to form compact aggregations resembling schools of fish. A similar induced behaviour may have occurred with our yellow perch.

Considering the extensive utilization of in-tank cover by the yellow perch, it is notable that no significant differences were seen in the survival of the fish in its absence. Apparently the formation of dense stationary schools was sufficient to conserve energy reserves. Under natural field conditions, the constant activity of the white perch would probably make them more susceptible to predation, while the inactivity, schooling, and cover-seeking behaviour of the yellow perch would lower their predation risk, further contributing to differences in overwinter survival of the two species.

Morphological differences between white perch and yellow perch result in larger differences in overwinter survival than is suggested by the overwinter survival models alone. At a common body length, white perch weigh more, indicating that they contain more energy per unit length. Even with these additional energy reserves, however, white perch died before yellow perch of the same length. Surviving white perch had consumed 8% more dry weight than surviving yellow perch at 2.5°C. Interspecific differences in routine metabolic rate and activity appear to account for this disproportionate consumption of energy.

White perch held at 2.5°C metabolized just over half the energy stores of white perch of similar size held at 4.0°C, yet they died before those held at 4.0°C. This suggests that death at 2.5°C is not caused by starvation but that other physiological factors are involved. Hunt (1969) and Oliver et al. (1979) have also observed an increase in the overwinter mortality at lower temperatures when studying brook trout and smallmouth bass, respectively. Changes in membrane permeability and impaired functioning of ion transport mechanisms at lower temperatures generally reduce the ability of fish to osmoregulate (Morris and Bull 1968; Stanley and Colby 1971; Davis and Simco 1976). Parvatheswararao (1970) and Nordlie and Leffler (1975) have suggested impaired osmoregulatory ability as a reason for

reduced survival of fish at low temperatures. For yellow perch, no significant mortality was noted at 2.5°C compared with the 17.7% mortality observed at 4.0°C; however, the yellow perch tested at 2.5°C were larger than those tested at 4.0°C by Post and Evans (1989). The colder temperature, however, did not appear to cause a dramatic increase in mortality as was the case for white perch, suggesting that cold temperature is not as debilitating for overwintering YOY yellow perch.

In the Bay of Quinte, Lake Ontario, a near collapse of white perch stocks occurred following the severe winter of 1977–78 (mean water temperature = 0.75°C, mean winter duration at or below 1.0°C = 98 d), while yellow perch stocks actually increased (Hurley 1986a). These observations support our conclusion that white perch are much less tolerant to severe cold temperatures than are the native yellow perch. To the present day, white perch have failed to regain their precrash dominance in the Bay of Quinte. One hypothesis to explain this shift in species dominance comes from Svardson's (1976) and Skud's (1982) analyses of environmental factors governing dominance in fish. Prior to 1978, a series of warm summers and relatively mild winters favoured the dominant white perch, allowing them to proliferate in the Bay of Quinte and maintain the yellow perch at a lower relative abundance. However, following the climate-related collapse of the white perch (Johnson and Evans 1990), the yellow perch became dominant over the white perch. Even though the mild winters now favoured the white perch, they have been unable to regain their dominance. Changes in the dominance hierarchy not only explains why the response of a species changes from positive to negative, but also why different stocks may not respond the same way to temperature (Skud 1982). An alternative hypothesis is that resurgence of the native walleye stock (increased predation pressure) combined with strong year-classes of yellow perch has increased competition for food and space, preventing the white perch from reestablishing their dominance in the Bay in Quinte.

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Prey-Size Relationships and Feeding Tactics of Primitive Stream-Dwelling Darters

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Rakocinski, C. 1991. Prey-size relationships and feeding tactics of primitive stream-dwelling darters. Can. J. Fish. Aquat. Sci. 48: 681–693.

Prey-size use and feeding tactics varied among three cooccurring darter species in the primitive subgenus *Hadropterus* (genus *Percina*). These darters span a wide range of body sizes, yet they all utilize the same lotic prey-size spectrum. An optimal-diet index (ODI) showed that small darters had more optimal diets than large darters. However, decelerating ODI curves showed that ontogenetic shifts occurred from number-maximizing to prey-size selective feeding tactics. Interspecific differences in feeding tactics, as characterized by differences in prey size, diet breadth, and numbers of prey, also were reflected by differences in slopes of ODI power curves. *Percina nigrofasciata* showed a relatively prey-size selective tactic; *P. sciera* showed a relatively number-maximizing tactic. In darters, prey-size selection corresponded with a broad diet and number maximizing corresponded with a narrow diet. When *P. nigrofasciata* were compared among four Black Creek sites, relatively optimal diets were found at two sites where large macroinvertebrates also were relatively abundant, as predicted from optimal foraging theory. However, only small differences in ODI values existed between two sites showing the greatest disparity in macroinvertebrate abundance. Prey size was an important diet characteristic related to the feeding tactics of particulate-feeding darters.

La taille des proies préférées et la stratégie alimentaire varient chez trois espèces de dards du sous-genre primitif *Hadropterus* (genre *Percina*). Même si la taille de ces dards varie grandement, ils consomment tous des proies lotiques d'un même écart de taille. Un indice du régime alimentaire optimal (ODI) a révélé que le régime alimentaire des petits dards est optimal par rapport aux gros dards. Toutefois, les courbes ODI à pente décroissante révèlent qu'il s'effectue des modifications ontogénétiques de la stratégie alimentaire, soit d'une maximisation du nombre de proies au choix de la taille des proies. Des différences interspécifiques de la stratégie alimentaire, y compris des différences de la taille, de la variété et du nombre de proies, étaient exprimées par des différences de la pente des courbes de puissance ODI. *Percina nigrofasciata* a choisi ses proies selon la taille, tandis qu *P. sciera* a favorisé la maximisation du nombre de proies. Chez les dards, le choix d'une proie selon la taille correspond à un régime alimentaire général tandis que la maximisation du nombre de proies correspond à un régime alimentaire restrient. La comparaison de quatre groupes de *P. nigrofasciata* du ruisseau Black a révélé que deux de ces groupes avaient un régime alimentaire optimal car leur habitat s'abritait de gros macroinvertébrés relativement abondants, comme l'avait prédit la théorie de la recherche optimale de nourriture. Toutefois, les valeurs ODI variaient peu à deux endroits où l'abondance des macroinvertébrés était nettement inégale. La taille des proies était une importante caractéristique du régime alimentaire liée à la stratégie alimentaire des dards s'alimentant de façon sélective.

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In this paper, I examine ontogenetic, interspecific, and ecotopic variation in prey-size use and feeding tactics within the primitive darter subgenus *Hadropterus* (Percidae, Etheostomini). Three *Hadropterus* species cooccur in southern Mississippi, including two common species, *Percina nigrofasciata* (blackbanded darter) and *P. sciera* (dusky darter). A third less-comon species, *P. lenticula* (freckled darter), is the largest and most primitive darter species (Page 1983). All sizes of darters depend upon the same size spectrum of small benthic macroinvertebrates, most of which are smaller than 5 mm (Page 1983). Prey-size use by darters is especially interesting because derived species may have evolved small body sizes to achieve an efficient prey-size relationship with the lotic prey-size spectrum (Page and Swofford 1984). However, darters span a wide range of body sizes. The largest species reaches a size roughly two orders of magnitude larger in mass (i.e. 70 g, 168 mm) than the smallest species (i.e. 0.6 g, 36 mm).

Although all darters show a particulate-feeding mode, wide body-size variation among darters suggests that they may demonstrate interesting variation in feeding tactics (i.e. alternative means of food selection). Two simple diet models define opposing feeding tactics for particulate feeders (Hodgson and Kitchell 1987). The functional response model predicts a numerical feeding response (i.e. number-maximizing tactic) with increasing prey abundance or predator size (Griffiths 1975). Conversely, the optimal-diet model predicts a prey-size selective response (Schoener 1971; Pyke 1984). According to the latter model, in order for predators to maximize their rate of energy gain, they should bypass small prey below some threshold value (i.e. foraging time/return). Energetic constrains imposed by the prey-size spectrum may limit the body size of a number maximizer. However, ontogenetic prey-size selection can foster growth to larger sizes than can be attained by a numerical response (Paloheimo and Dickie 1966).

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Feeding tactics may vary in biologically meaningful ways for darters. An ontogenetic shift from number maximizing to prey-size selection might enable darters to grow large. The feeding tactics of closely related darter species may differ enough to allow their coexistence. Feeding tactics may vary ecotopically (i.e. regionally among sites) with prey abundance in ways that concur with foraging theory. In this paper, I address three questions about variation in feeding tactics among primitive darters: (1) Do ontogenetic shifts in diets and feeding tactics occur? (2) Do diets vary between darter species in ways that characterize different feeding tactics? (3) Do diets vary ecotopically with macroinvertebrate abundance in ways that support or refute predictions from optimal-diet models?

Materials and Methods

Field Methods

To examine diet variation, I took samples of *Percina* and macroinvertebrates from seven stream sites at similar latitudes (31°00′ to 31°25′N). The sites were on second- to fourth-order streams within the Pine Hills physiographic region of the Mississippi coastal plain. In this region, streams are typically of low gradient with sand, gravel, or clay substrates. The sites were forested by either pine woods or bottomland hardwoods and streams contained scattered woody debris.

Darter populations and habitat structure varied among sites (Rakocinski 1988). *Percina* were abundant: density estimates ranged between 0.24 and 1.31/m^2. At the most upstream site on Perkins Creek (Lamar County), *P. nigrofasciata* was the only *Hadropterus* species present. *Percina nigrofasciata* outnumbered *P. sciera* at four sites on the upper mid- to lower midreaches of Black Creek (Forrest and Perry counties). Higher relative abundances of *P. sciera* and larger darters occurred both at one site on lower Tallahala Creek near its confluence with the Leaf River (Perry County) and at another site on the east fork of the Amite River near Gilsburg, MS (Amite County, Ponchartrain drainage). Except for the latter site, all sites were within the Pascagoula River drainage.

Darters were collected for diet analysis with dipnets from the seven stream sites during the late summer or early autumn (i.e. late August to early October 1981 and 1982). During sampling, stream flow was stable and turbidity low (i.e. Secchi disk > 1 m). Sampling was initiated about 2.0–2.5 h before sunset, a diurnal peak in feeding by *Percina* (Mathur 1973 and pers. obs.). Samples for diet analysis included between 20 and 50 darters from each site. Tricaine methanesulfonate (i.e. MS 222) was used to anaesthesize darters before they were injected intraperitoneally and fixed with 10% formalin.

To measure relative abundances of macroinvertebrates among the seven stream sites, I took diurnal and nocturnal drift samples (cf. Mathur 1973). Two 200-μm drift nets 32 cm in diameter were placed together at the downstream ends of sites. Nets were completely submerged, while they rested between 10 and 15 cm above the substrate. Diurnal drift was sampled for 3 h immediately before darters were collected. Nocturnal drift was sampled for between 40 and 60 min (i.e. usually 55 min) following dusk, a peak diel period of drifting by lotic macroinvertebrates (Waters 1972).

To consider diets of very large darters, I examined 10 *P. lenticula* from four additional collections belonging to the University of Southern Mississippi Fish Collection and the Mississippi Fish and Game Commission. These fish were collected in southern Mississippi between summer 1978 and autumn 1983 by either rotenone or seine. The 13 *P. lenticula* examined in this study ranged between 3.37 and 44.72 g wet mass (i.e. 67.6–157.0 mm standard length).

Laboratory Methods

Before dissecting darters, I measured standard length (SL), head length (HL), and mouth width (MW) to the nearest 0.1 mm with dial calipers. The blotted wet mass of specimens was weighed to the nearest 0.01 g using a Mettler model P1200 electrobalance. During dissection, I examined the digestive tract from the esophagus to the first bend in the intestine. Food items were sorted into major taxa (i.e. usually genus or family), enumerated, and measured to the nearest 0.1 mm with an ocular micrometer. Sizes of incomplete prey were estimated by comparing them with items of known sizes.

Although hydroptilid larvae (i.e. microcaddisflies) often occurred in guts without cases, I assumed that all larvae were ingested with intact cases and that missing cases were expelled during handling because larvae of similar sizes also were usually present with cases. Length estimates of missing cases were based on extant measurements.

To provide a common measure of prey size, I used length/mass equations to estimate sizes of individual prey and macroinvertebrates from drift samples. Length/mass equations were based on freshly preserved (i.e. 45–95% isopropanol) macroinvertebrates from drift samples and extraneous benthic collections. Depending on the kind of macroinvertebrate, I consistently measured body length, pronotal length, or head-capsule length to the nearset 0.1 mm using an ocular micrometer. Premeasured macroinvertebrates were dried for 27–52 h at 60–70°C, before weighing them to the nearest 0.1 μg on a Mettler M5 microbalance. Each measurement of macroinvertebrate mass consisted of the combined weight of between 1 and 30 individuals of a given prey type and size class.

Macroinvertebrate length/mass data contributed to 37 significant equations (i.e. $N = 5$–27), representing all major prey types (Rakocinski 1986). The linearized length/mass equation was $\ln W = \ln a + b \ln L$ where W is micrograms dry mass, L is the linear measurement (millimetres), and a and b are constants. Average weights furnished estimates for prey taxa that did not vary in size. Dry mass estimates for several rare prey types were made from a general length/mass equation obtained by averaging coefficients from equations for 15 common prey types. This equation was $\ln W = -12.96 + 2.76 \ln L$. Finally, some obscure prey types were directly weighed.

Three measures of darter body size were interrelated for this study, including SL of preserved fishes, SL of living fishes, and wet weights of preserved fishes. Length/weight equations fit very closely as a power function for all three darter species ($r > 0.99$, $P < 0.001$). As shown by a lower intercept, *P. sciera* were more streamlined than *P. nigrofasciata* over the size range examined ($t = 12.56$, $P \ll 0.001$, $b_c = 3.22$). Preserved SL versus live SL relationships also were significant for these two species ($r > 0.99$, $P < 0.001$).

Handling-Time Trials

To determine handling-time equations for the three darter species, I conducted feeding trials with darters in aquaria. Individual subjects included 14 *P. nigrofasciata* ranging between 0.35 and 4.08 g wet mass, 14 *P. sciera* ranging between 0.08 and 3.74 g wet mass, and one *P. lenticula* of 6.40 g wet mass.

TABLE 1. General handling-time equations for the three darter species. The model $y_i = 0.83 + ae^{bx_i}\epsilon_i$, was fit in its linearized form. OPT = optimum, h = seconds handling time, x_i = (prey dry mass/darter wet mass) $\times 10^5$, OPT h/x_i = cost-curve minimum, ***$P<0.0001$, r = correlation coefficient.

Species	N	b	a	r	P	OPT h/x_i	OPT h	OPT x_i
P. nigrofasciata	191	0.061	3.39	0.82	***	0.61	10.8	17.7
P. sciera	293	0.045	4.48	0.81	***	0.58	13.7	23.7
P. lenticula	26	0.048	4.01	0.87	***	0.56	12.5	22.4

Premeasured live prey were presented individually to isolated fishes to provide handling-time data. Handling time was recorded as the duration between initial prey contact and the resumption of darter respiration, when uninterrupted by swallowing movements for at least 1 min. Following the rationale of Werner (1974), feeding trials did not exceed 12 prey items per darter, to avoid satiation effects. Following each trial, I anesthetized the darter and measured its SL.

A total of 566 handling-time observations were obtained from 147 feeding trials including a wide array of shapes, sizes, and kinds of prey. Prey types included various ephemeropteran, plecopteran, and odonate nymphs, as well as trichopteran and dipteran larvae. To determine general handling-time equations for darters, I pooled data for all prey types for each darter species. Comparisons of handling-time curves were not made among different prey types because different prey types can occur over widely different size ranges. However, since hellgrammite larvae were exceptionally heavy bodied, I treated them separately. The dry mass of prey typically varied from small 0.6-μg chironomid larvae to large 3406-μg plecopteran nymphs whereas hellgrammite dry mass ranged between 564 and 15 643 μg.

Optimal-Diet Index

Handling-time data were fit by the model $y_i = 0.83 + ae^{bx_i}\epsilon_i$ where y_i is the average handling time for the ith relative prey size, x_i is the ith relative prey size (i.e. (prey dry mass/darter wet mass) $\times 10^5$), a and b are constants, and ϵ_i is the multiplicative error variance (Werner 1974). To estimate the baseline handling time of 0.83 (SD = 0.14, n = 7), I averaged values that were less than 1 s in duration. Linearized handling-time equations were highly significant for all three darter species (Table 1). More than 64% of the variance in transformed handling times was accounted for by relative prey size.

Handling time increased with relative prey size at different rates for the darter species (Table 1). *Percina nigrofasciata* had a steeper curve than did the more slender *P. sciera* ($P < 0.001$, t-test). Although the *P. lenticula* equation was based on only one individual, the equation for this species appeared to be accurate because *P. lenticula* constants fell between those of the other two darter species (Table 1.)

Darter handling-time equations were used to calculate cost curves that described the change in prey value (i.e. foraging time/return) as relative prey size increases. Values of various prey sizes were estimated by ratios of handling time (i.e. h, in seconds) to relative prey mass (i.e. x_i, prey mass/darter mass) as a measure of return (Werner 1977; Bannon and Ringler 1986). As expected, cost curves of h/x_i versus x_i were U-shaped (Fig. 1A and 1B) (cf. Werner 1977). At first, cost curves decreased with increasing return (x_i) to a minimum, the optimum prey size (OPS), and thereafter, curves increased exponentially with handling time (h).

The entire prey-size composition of each darter was evaluated using the OPS as a standard of comparison. The optimal-diet index (ODI) was defined as the average deviation in value of all prey from the OPS, scaled to the value of the OPS (i.e. h/x_{OPS}):

$$(1)\quad ODI = \Sigma\,[(h/x_i - h/x_{OPS})/(h/x_{OPS})]/n$$

where n is the number of prey in the diet. Because the index is scaled to the value of the OPS, it expresses the magnitude of deviation from the value of the OPS as a multiple of the OPS value. Thus, an ODI of 10 connotes a prey-size composition that is 10-fold less valuable than a diet composed exclusively of optimum prey sizes.

Exploring hypothetical ODI relationships provided a means to identify different darter feeding tactics. For a diet made up exclusively of a single prey size, the ODI forms a hairpin-shaped curve as darter size increases (Fig. 1C). A minimum ODI of zero corresponds to the optimum darter size, and the steep rise in the curve preceding the minimum ODI reflects gape limitation. As darter size increases beyond the minimum ODI, the index is initially driven both by decreasing handling time (i.e. h) in the numerator and decreasing return (i.e. x_i) in the denominator. However, once the minimum handling time is reached, the ODI is driven solely by a linear decrease in relative prey size. This results in a nearly linear divergence of the ODI away from zero with increasing darter size.

Simulated ODI curves based on a single prey size typically displayed slopes that were near 1.0 for darter sizes larger than the optimum size. If darters of all sizes indiscriminantly consume all sizes of prey, ontogenetic ODI curves should usually have slopes approaching 1. This is because small prey regularly occur in geometrically greater numbers than large prey in aquatic systems (Mittelbach 1981a). Alternatively, if feeding tactics shift ontogenetically, from a numerical response to an optimal-diet response, slopes of ODI power curves should be considerably less than 1.

Data Analyses

Several measures characterized diets of individual darters. Because prey-size distributions were lognormal, the geometric mean prey size (i.e. microgram dry mass) was used as a central measure of prey-size use. Maximum and minimum prey sizes also were determined for each darter. Prey-size diversity and prey-taxon diversity were calculated to measure different aspects of diet breadth. Diet diversity was obtained using the Shannon index, $H' = -\Sigma\, p_i \log p_i$, where p_i represents the proportion made up by category i (Zar 1984). Finally, the number and biomass of prey also were quantified for each darter.

Several measures characterized entire samples. For both diet and drift samples, I calculated numerical and gravimetric proportions (p_i) made up of various macroinvertebrate taxa. Gravimetric proportions were based on dry mass estimates from length/weight equations. Several indices were calculated using p_i. Schoener's (1968) formula, $\Sigma|p_{ij} - p_{ik}|$ (where j and k = darter species), summarized interspecific overlap (α), Levins' (1968) formula, $1/\Sigma p_i^2$, summarized diet breadth (B), and the Shannon index, $-\Sigma p_i \log p_i$, summarized diet diversity (H') (Zar 1984).

Power curves of several diet measures verses darter size described ontogenetic diet changes. Various diet measures were

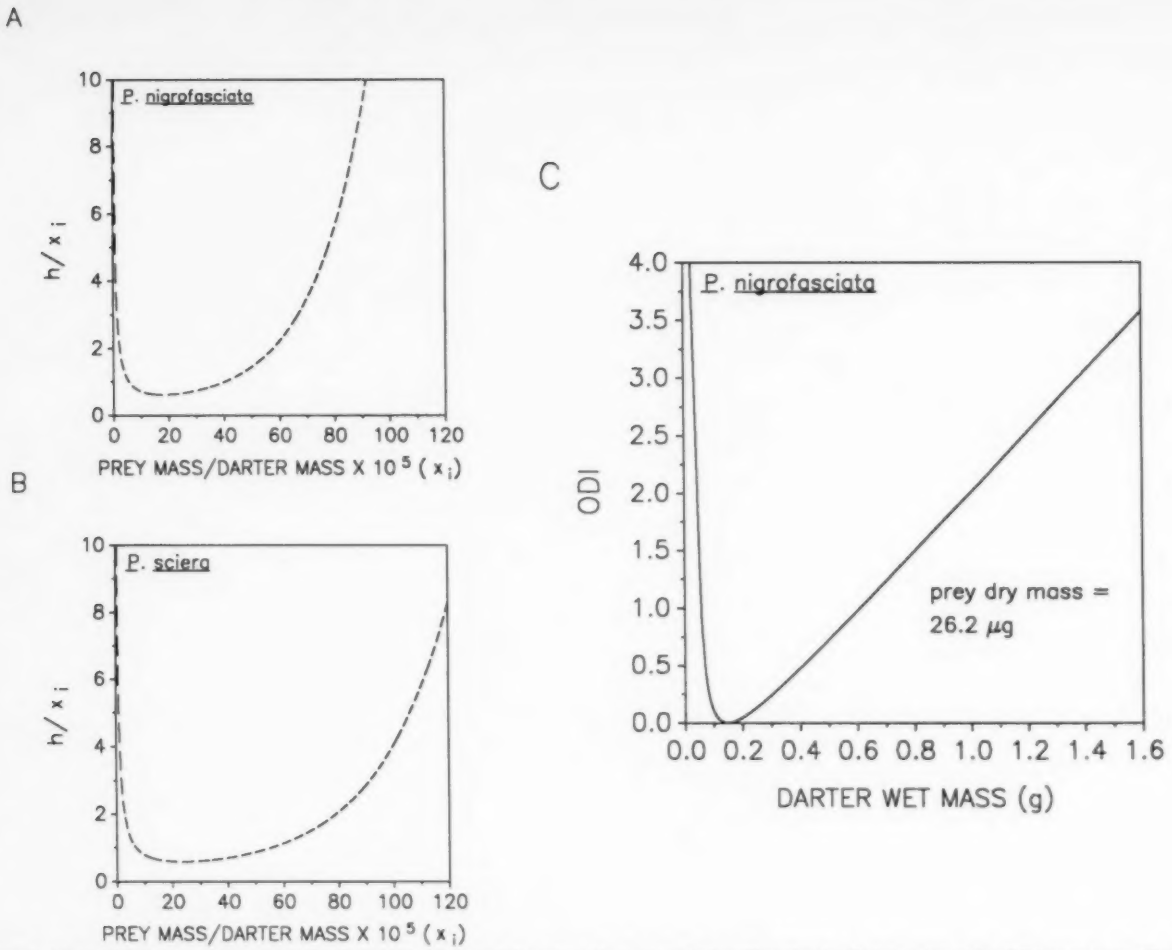

FIG. 1. (A and B) General cost curves for *P. nigrofasciata* and *P. sciera* (h = seconds handling time); (C) behavior of the ODI over a specified range of darter sizes, assuming a constant prey size of 26.2 μg dry mass and *P. nigrofasciata* handling-time coefficients.

regressed on darter size (i.e. ln wet mass), including geometric mean, maximum, and minimum prey sizes (i.e. micrograms dry mass), as well as the number of prey, prey biomass, and the ODI. Asymptotic curves of diet diversity were fit by the linear form of the equation $H' = ae^{b/x}$ where a and b are constants and x is darter size. A quadratic equation provided the best fit for the number of prey (i.e. ln N + 1) versus darter-size relationship of *P. nigrofasciata*. Relationships having F-ratios (regression SS/total SS) occurring at $P < 0.05$ were considered significant. Regression F-tests were made using the software package BIOΣTAT, and Dixon's tests were used to identify occasional outliers for removal (Pimentel and Smith 1986).

To make effective parametric comparisons between *P. nigrofasciata* and *P. sciera*, samples of these species from four midreach sites on Black Creek were routinely pooled. Sample sizes of the *P. nigrofasciata* varied between 30 and 39, while sample sizes of *P. sciera* varied between 9 and 16. Sizes of the total 141 Black Creek *P. nigrofasciata* ranged between 0.10 and 5.18 g wet mass (22.6–72.9 mm SL), while sizes of the 46 total Black Creek *P. sciera* ranged between 0.32 and 4.25 g wet mass (31.6–71.8 mm SL).

ANCOVA was used to examine variation among individual samples of *P. nigrofasciata* and between darter species (Pimentel and Smith 1986). When slopes were not different, the ANCOVA output appropriately tested the equality of adjusted means. Where more than two simultaneous comparisons were necessary, multiple comparisons were made among slopes using both the GT2 and T' methods (Sokal and Rohlf 1981). When confidence limits of slopes overlapped and adjusted means were different, Student–Newman–Keuls tests provided multiple comparisons among adjusted means. Tests of hypotheses about individual slopes were provided by t-tests (Zar 1984). Nonparametric Wilcoxon-matched pairs tests, including all pairs of individual samples with both common darter species, were occasionally used to confirm the findings from parametric tests (Siegel 1956).

Comparisons among samples of *P. nigrofasciata* and drifting macroinvertebrates from various sites helped to assess ecotopic diet variation. Nonparametric Spearman rank correlations and Kendall's tests of concordance elucidated how macroinvertebrate drift flux and diets covaried (Siegel 1956). ODI relationships of Black Creek samples were compared using ANCOVA and examined with respect to macroinvertebrate abundance to

TABLE 2. Predator–prey relationships for pooled samples of *P. nigrofasciata* and *P. sciera* from Black Creek and pooled *P. lenticula*. b = slope of linearized relationship, S_b = standard error of the slope, int = intercept of linearized relationship, *P.n.* = *Percina nigrofasciata*, *P.s.* = *Percina sciera*, *P.l.* = *Percina lenticula*, ***$P < 0.0001$, **$P < 0.01$, *$P < 0.05$, NS = nonsignificant, geom mps = geometric mean prey size, max ps = maximum prey size, min ps = minimum prey size, asym ps div = asymptotic prey-size diversity, asym pt div = asymptotic prey-type diversity, (N + 1) = number of prey plus 1, prey mass = total prey mass, ODI = optimal-diet index.

Relationship	Species	N	r	b	S_b	P	int	Fig.
ln geom mps	*P.n.*	141	0.77	0.68	0.05	***	2.52	2A
ln geom mps	*P.s.*	46	0.62	0.36	0.07	***	2.40	2B
ln geom mps	*P.l.*	13	0.62	0.45	0.17	*	2.72	
ln max ps	*P.n.*	141	0.65	1.00	0.10	***	5.32	
ln max ps	*P.s.*	46	0.51	0.79	0.20	***	4.62	
ln max ps	*P.l.*	13	0.66	0.91	0.31	*	4.30	
ln min ps	*P.n.*	141	0.50	0.73	0.11	***	−0.06	
ln min ps	*P.s.*	46	0.05	0.09	0.26	NS	0.10	
ln min ps	*P.l.*	13	0.52	1.03	0.51	NS	−1.39	
asym ps div	*P.n.*	140[a]	0.52	−0.22	0.03	***	−0.39	
asym ps div	*P.s.*	46	0.44	−0.15	0.05	***	−0.47	
asym ps div	*P.l.*	13	0.31	−0.68	0.63	NS	−0.13	
asym pt div	*P.n.*	140[a]	0.40	−0.12	0.02	***	0.24	2C
asym pt div	*P.s.*	46	0.00	0.01	0.05	NS	−0.30	2D
asym pt div	*P.l.*	13	0.47	−2.10	1.20	NS	0.31	
pt div/ps div	*P.n.*	140[a]	0.76	0.41	0.03	***	0.06	
pt div/ps div	*P.s.*	46	0.18	0.12	0.08	NS	0.44	
pt div/ps div	*P.l.*	13	0.67	0.35	0.11	*	0.45	
ln (N + 1)	*P.n.*	141[b]	0.00	−0.02	0.08	NS	3.51	2E
ln (N + 1)	*P.s.*	46	0.41	0.61	0.20	***	3.76	2F
ln (N + 1)	*P.l.*	13	−0.17	−0.16	0.27	NS	4.31	
ln prey mass	*P.n.*	141	0.59	0.77	0.09	***	6.82	
ln prey mass	*P.s.*	46	0.64	0.99	0.18	***	6.63	
ln prey mass	*P.l.*	13	0.57	0.79	0.35	**	6.60	
log ODI	*P.n.*	141	0.42	0.35	0.06	***	1.06	
log ODI	*P.s.*	46	0.70	0.65	0.10	***	1.11	
log ODI	*P.l.*	13	0.57	0.59	0.25	*	0.99	
log ODI	*P.s./P.l.*	58[a]	0.83	0.54	0.05	***	1.11	

[a]Zero values or outliers excluded.
[b]Quadratic relationship significant.

address predictions of the optimal-diet model. Darter samples also were directly compared from two sites with the widest extremes in macroinvertebrate abundance.

Results

Ontogenetic Variation

Generally, prey size increased with darter size. For example, both geometric mean and maximum prey size increased significantly with darter size for all three darter species (Table 2; Fig. 2A). All seven samples of *P. nigrofasciata* examined had significant geometric mean prey-size relationships ($P < 0.001$, F-ratio). Despite the small sample size, both mean and maximum prey-size relationships were significant for the pooled *P. lenticula* sample, indicating that prey size continued to increase up to the largest darter sizes. Maximum prey-size slopes were not different from 1 for Black Creek *P. nigrofasciata* or *P. sciera* ($P < 0.05$, t-tests), implying that maximum prey size reflected gape limitation. Minimum prey size was more variable. Black Creek *P. nigrofasciata* was the only pooled sample that was significant for minimum prey size.

Prey-size and prey-type diversity changed asymptotically with darter size (Table 2; Fig. 2). These asymptotic increases in diet diversity might have resulted either from the relatively low availability of large prey types or from large fish bypassing relatively numerous small prey types.

Despite wide variation in ODI values (i.e. ODI = 0.5–355), a general ontogenetic shift in darter feeding tactics, from number maximizing to prey-size selection, was revealed by ODI curves (Table 2; Fig. 3). Slopes of ODI power curves for seven individual samples of *P. nigrofasciata* were all significantly less than 1 (i.e. b = 0.27–0.63) ($P < 0.05$, t-tests), indicating that ODI curves leveled off. Slopes for pooled *P. nigrofasciata* and *P. sciera* also were less than 1 ($P < 0.001$, t-tests). Ascending limbs of ODI curves reflected a numerical response over the underlying range of darter sizes, and descending limbs indicated prey-size selection by larger darters. Actual ODI values for large *P. nigrofasciata* of 5 g wet mass averaged threefold lower than expected, assuming a number-maximizing tactic (i.e. slope = 1) (Fig. 3). The diet of a medium-sized *P. nigrofasciata* of 1 g wet mass averaged 10 times lower in value than an optimal diet (i.e. ODI = 10).

As a rule, small darters had more optimal diets than large darters, probably due to their better positions in relation to the prey-size spectrum (Fig. 3). For example, the diet of a large *P. nigrofasciata* of 5 g wet mass was fourfold less optimal than that of a small juvenile *P. nigrofasciata* of 0.1 g wet mass (i.e. ODI = 20 and 5, respectively).

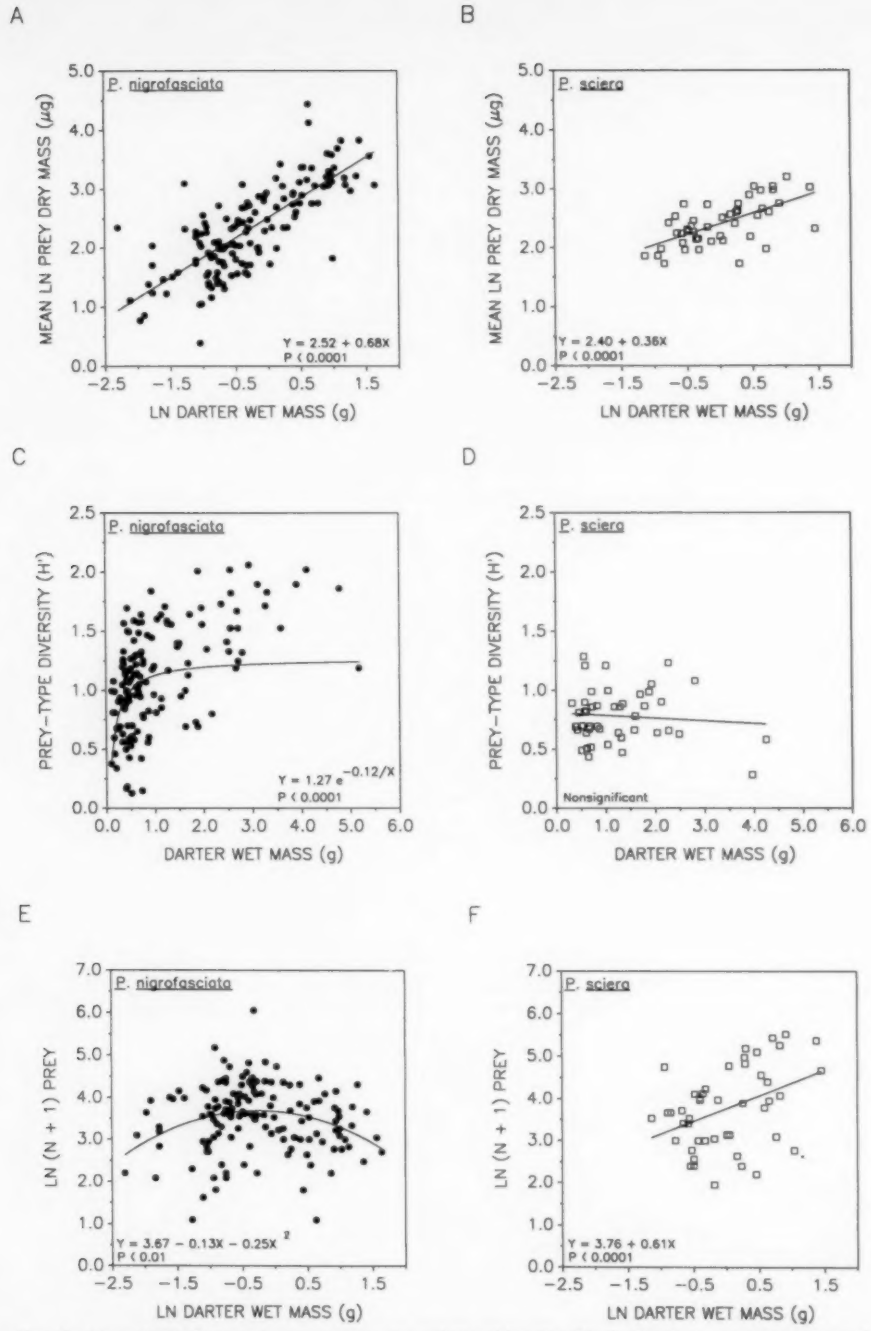

FIG. 2. (A and B) Geometric mean prey-size relationships for Black Creek *P. nigrofasciata* and *P. sciera*; (C and D) prey-type diversity relationships for Black Creek *P. nigrofasciata* and syntopic *P. sciera*; (E and F) prey-number relationships for Black Creek *P. nigrofasciata* and syntopic *P. sciera*.

Ontogenetic prey-size selection continued up to the largest darter sizes, represented by *P. lenticula* as large as 45 g wet mass (Table 2; Fig. 3B). This was shown by a composite ODI curve including all Black Creek *P. sciera* and *P. lenticula* ($P < 0.0001$, F-ratio). The ascending limb of the curve depicted a rapid increase in ODI values for *P. sciera* up to 4.5 g wet mass. By contrast, the descending limb of the curve showed continued ontogenetic prey-size selection, over another order of magnitude in size, by *P. lenticula* between 4 and 45 g wet mass. This implied that large darters continually shifted along the prey-size spectrum to use increasingly larger and rarer prey as they grew.

Ontogenetic change in prey-size use also corresponded with concomitant shifts in prey-type use. For example, 90% of the

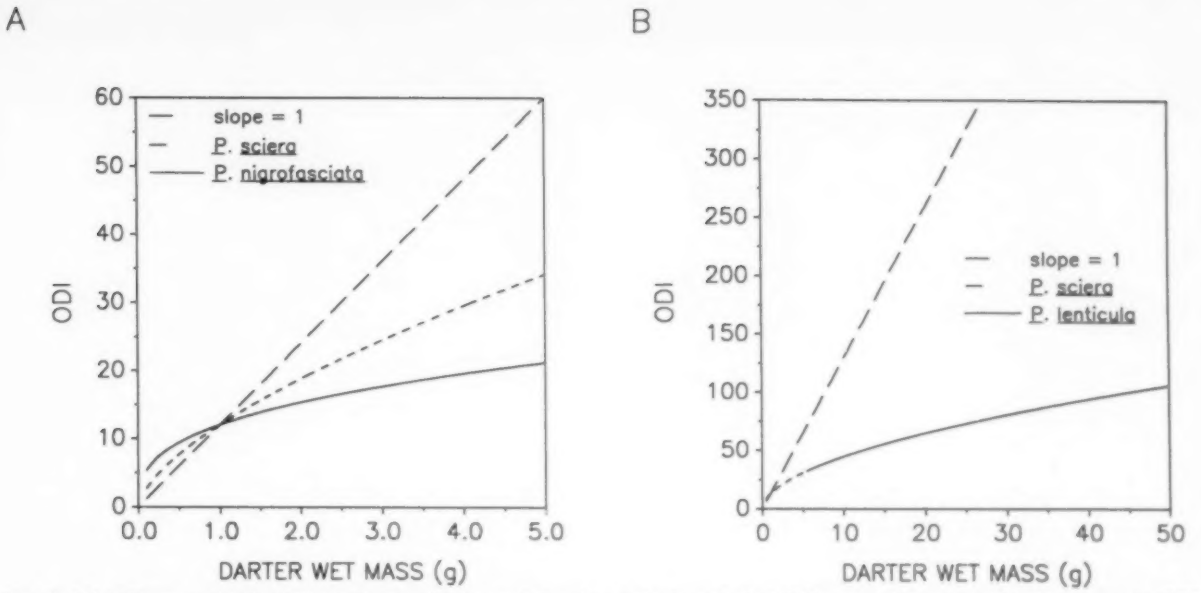

FIG. 3. (A) ODI curves for Black Creek *P. nigrofasciata* and *P. sciera* and a hypothetical ODI curve with a slope of 1; (B) composite ODI curve for Black Creek *P. sciera* and *P. lenticula*.

diet volume of *P. lenticula* consisted of large prey types, such as heptageneids, isonychids, hydropsychids, philapotomids, odonates, plecopterans, and hellgrammites. By contrast, these same large prey made up only 41 and 20% of the diet volumes of Black Creek *P. nigrofasciata* and *P. sciera*, respectively.

Interspecific Variation

Diets differed between syntopic *P. nigrofasciata* and *P. sciera* in ways that indicated different feeding tactics. Ontogenetically, *P. nigrofasciata* showed a stronger prey-size selective response whereas *P. sciera* displayed a stronger numerical feeding response. As a corollary, diets were broader for *P. nigrofasciata* than for *P. sciera*.

Typically, *P. nigrofasciata* consumed larger prey than did *P. sciera*. Geometric mean prey size (micrograms dry mass) increased faster with darter size (grams wet mass) for *P. nigrofasciata* than for *P. sciera*. This was conveyed by a significantly steeper slope for Black Creek *P. nigrofasciata* compared with syntopic *P. sciera* (Fig. 2A and 2B; Table 2). Confidence intervals of slopes for four individual samples of Black Creek *P. nigrofasciata* overlapped broadly (N = 30–39) ($P > 0.25$, F-ratio). However, the common slope of Black Creek *P. nigrofasciata* was almost twice as steep as that of *P. sciera* (N = 46) (i.e. slopes = 0.68 versus 0.36) ($P < 0.0001$, F-ratio).

For mean prey size as well as a few other measures of prey use, the residual mean squares was higher for *P. nigrofasciata* than for *P. sciera*. Thus, for these relationships, the variance was also probably greater for *P. nigrofasciata* than for *P. sciera*. For example, the residual mean squares for mean prey size was almost twice as great for the former species (0.23 versus 0.09) ($P < 0.001$, chi-square). However, since the pooled sample size for *P. nigrofasciata* was threefold greater than for *P. sciera* (i.e. 141 versus 46), the effects of disparate variances on interspecific parametric tests were conservative (Zar 1984).

In addition to mean prey size, maximum and minimum prey size (micrograms dry mass) also differed between darter species, but in different ways. Again, confidence intervals of maximum prey-size slopes overlapped broadly among all four individual samples of Black Creek *P. nigrofasciata* ($P > 0.6$, F-ratio). The common slope for Black Creek *P. nigrofasciata* was equal to 1 (Table 2), implying that maximum prey mass increased at the same rate as darter mass. Although the slope for Black Creek *P. sciera* was lower than for *P. nigrofasciata*, there was no significant difference in slopes between the two darter species ($P > 0.6$, F-ratio). However, adjusted means were different between species (5.11 versus 4.42) ($P < 0.001$, F-ratio), indicating that *P. nigrofasciata* consumed larger maximum prey sizes (micrograms dry weight) than did syntopic *P. sciera* of equal mass.

Minimum prey size usually increased significantly with darter size for *P. nigrofasciata*. Three of the four samples of *P. nigrofasciata* from Black Creek were significant for minimum prey size ($P < 0.001$, F-ratio). Confidence intervals of the four slopes for Black Creek *P. nigrofasciata* overlapped ($P > 0.5$, F-ratio), and the common slope was 0.73 (Table 2). Although minimum prey size was significant for Black Creek *P. nigrofasciata* ($P < 0.0001$, F-ratio), it was nonsignificant for syntopic *P. sciera* ($P > 0.7$, F-ratio).

The generality of steeper mean prey-size slopes and higher maximum prey-size intercepts for *P. nigrofasciata* relative to *P. sciera* was corroborated by comparing six paired samples of both species using Wilcoxon matched pairs tests. The samples included four pairs from Black Creek and two pairs from Tallahala Creek and the Amite River. The samples from the latter two sites contained high relative abundances of *P. sciera* and exceptionally large darters of both species (Rakocinski 1986). These nonparametric tests showed that *P. nigrofasciata* consumed larger mean and maximum prey sizes than did syntopic *P. sciera* ($P < 0.05$).

Asymptotic prey-size diversity curves were significant, but not different between darter species. Slopes of linearized equa-

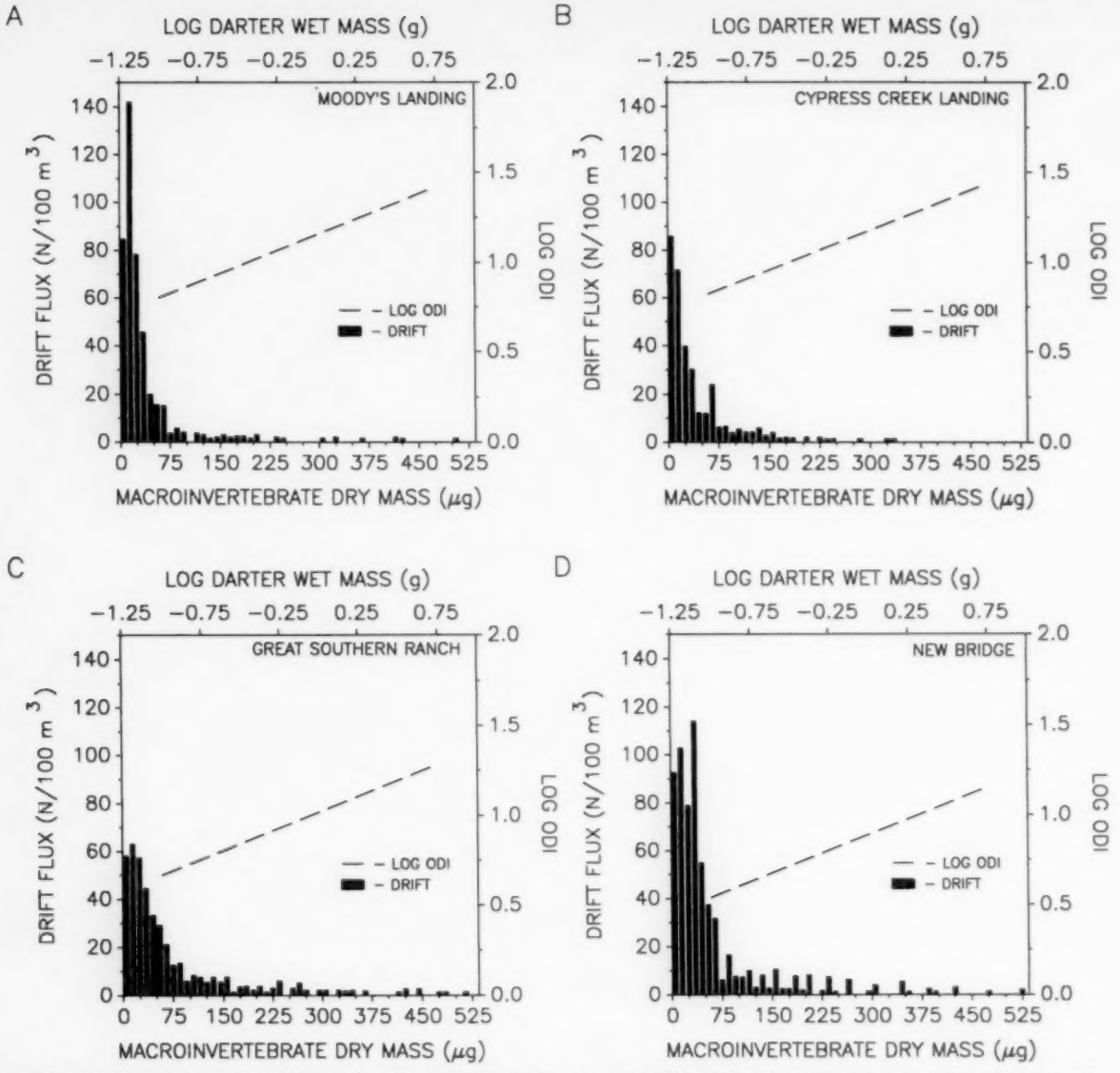

FIG. 4. Levels of macroinvertebrate drift distributed among various size classes and ODI relationships of four samples of *P. nigrofasciata* from Black Creek.

tions overlapped between the two common species from Black Creek ($P > 0.5$, F-ratio), and adjusted means were almost identical as well ($P > 0.9$, F-ratio) (Table 2). However, prey-type diversity was clearly different between darter species. Although Black Creek *P. nigrofasciata* had a strong asymptotic prey-type diversity relationship ($P < 0.0001$, F-ratio), syntopic *P. sciera* showed no relationship between prey-type diversity and darter size ($P > 0.9$, F-ratio), (Fig. 2C and 2D; Table 2). Prey-size diversity was directly correlated with prey-type diversity for Black Creek *P. nigrofasciata* ($P < 0.0001$, F-ratio). However, prey-type diversity did not increase with prey-size diversity for Black Creek *P. sciera* ($P > 0.16$, F-ratio).

Interspecific differences in the number and biomass of prey ingested further illustrated contrasting darter feeding tactics. The number of prey (i.e. $\ln N + 1$) changed quadratically with darter size for Black Creek *P. nigrofasciata* ($P < 0.01$, F-ratio) (Fig. 2E). By contrast, the number of prey increased linearly with darter size for Black Creek *P. sciera* ($P < 0.0001$, F-ratio) (Table 2; Fig. 2F). Both darter species showed positive relationships between total prey biomass and darter size ($P < 0.0001$, F-ratio). Moreover, neither slopes or adjusted means were different between darter species ($P > 0.65$, F-ratio, slopes; $P > 0.15$, F-ratio, adjusted means). This implied that as they grew large, *P. sciera* continued to gain prey biomass by eating more prey, while *P. nigrofasciata* ate fewer, but larger prey.

Ontogenetic ODI curves reflected interspecific differences in feeding tactics. A relative number-maximizing tactic was indicated by a high ODI slope for *P. sciera* whereas a stronger

prey-size selective tactic was shown by a relatively low slope for *P. nigrofasciata* (Fig. 3A; Table 2). The slopes of four individual samples of Black Creek *P. nigrofasciata* were not different ($P > 0.3$, F-ratio). However, the common slope for Black Creek *P. nigrofasciata* was significantly lower than the slope for syntopic *P. sciera* ($P < 0.05$, F-ratio). This implied that ODI values diverged faster (i.e. diets were less optimal) with increasing darter size for *P. sciera* than for *P. nigrofasciata*.

Interspecific differences in feeding tactics also were linked to differences in prey-type use. All major prey types were shared to some degree between darter species; however, each species concentrated on different prey types. Consequently, diet overlap was normally low between darter species. For example, interspecific volumetric diet overlap (α) among four Black Creek collections ranged between 0.27 and 0.60. Compared with syntopic *P. sciera*, Black Creek *P. nigrofasciata* ate twice the volume of small chironomid larvae (20 versus 10%) and large prey types (i.e. large ephemeropterans, trichopterans, odonates, plecopterans, and megalopterans) (41 versus 20%). By contrast, Black Creek *P. sciera* consumed more than three times the volume of small- and medium-sized baetid nymphs (34 versus 9%) and small simuliid larvae (20 versus 6%) than did syntopic *P. nigrofasciata*.

The diet of *P. nigrofasciata* was richer and broader than that of syntopic *P. sciera*. Diet richness for individual samples (N = 30–39) of Black Creek *P. nigrofasciata* ranged between 19 and 35 prey types whereas a grand total of 22 prey types occurred in the corresponding pooled sample of *P. sciera* (N = 46). Even samples from the Amite River, with especially large darters of both species, differed widely in diet richness (19 *P. nigrofasciata* = 30 prey types, 15 *P. sciera* = 15 prey types). *Percina nigrofasciata* usually surpassed *P. sciera* by a factor of two in volumetric diet breadth (B). Diet breadth was ony 3.81 for all 46 Black Creek *P. sciera* whereas diet breadth ranged between 6.94 and 7.44 for corresponding individual samples of *P. nigrofasciata* (N = 30–39). The broad diet of *P. nigrofasciata* probably resulted from contributions by infrequent large prey to diet volume.

Ecotopic Variation

Macroinvertebrate abundance varied considerably among sites. Nocturnal drift flux varied over an order of magnitude, ranging between 37 and 614/m^3. Moreover, among-site ranks of nocturnal drift flux agreed closely with ranks of diurnal drift flux ($r_s = 0.96$, $P < 0.0025$), implying that nocturnal drift accurately reflected among-site variation in macroinvertebrate abundance. Total drift flux was consistent with that of most prey types, including small and medium simuliid larvae and baetid nymphs, as well as large prey types, including various ephemeropterans, trichopterans, and plecopterans (Kendall's coefficient of concordance $W_c = 0.82$, $P < 0.01$). However, chironomid larvae drift rates were negatively correlated with total drift, although not significantly ($r_s = -0.36$, $P > 0.2$).

In some respects, prey-size relationships of *P. nigrofasciata* samples reflected the variation in drift flux. Maximum prey-size slopes were inversely related to levels of chironomid drift ($r_s = -0.89$, $P < 0.05$), perhaps because chironomid larvae were less abundant where large macroinvertebrates were abundant. Also, slopes of arithmetic mean versus standard deviation in prey-size relationships were correlated with drift flux ($r_s = 0.79$, $P < 0.05$). This probably reflected disproportionate effects by large prey on the average prey size where macroinvertebrates were abundant (Peters 1983).

Covariation between ODI relationships and macroinvertebrate abundances suggested a biologically meaningful pattern. Relatively high nocturnal drift flux occurred at the four Black Creek sites (i.e. 310–614/m^3), and macroinvertebrate size distributions from these sites had distinct peaks of small macroinvertebrates, less than 75 μg dry weight. However, macroinvertebrates larger than 75 μg were markedly more abundant at two of the sites than at the other two sites (i.e. 100 and 112/m^3 versus 40 and 39/m^3) (Fig. 4). Regressions of log ODI on log darter mass were significant for all four samples of Black Creek *P. nigrofasciata* ($P < 0.0001$, F-ratio). There was no difference among ODI slopes of the four samples of *P. nigrofasciata* ($P > 0.3$, F-ratio) ($b_c = 0.35$); however, there was a difference among adjusted means ($P < 0.0001$, F-ratio).

The same two sets of samples that were different in abundances of large macroinvertebrates also were distinguished by adjusted means of their ODI relationships (Fig. 4). Multiple comparisons of adjusted ODI means grouped the four samples into two different sets ($P < 0.05$, Student–Newman–Keuls tests) (i.e. adjusted means of log ODI = 0.85 and 0.98 versus 1.11 and 1.13). The same two sites with high drift rates of large macroinvertebrates also had relatively low adjusted ODI means. For example, the predicted ODI of a 1-g fish ranged between 12.9 and 13.4 from the two sites with lower abundances of large macroinvertebrates whereas it ranged between 7.0 and 9.5 from the two sites with higher abundances of large macroinvertebrates. Furthermore, the site with the highest abundance of large prey also had the lowest adjusted mean. This site had the highest drift rate of small (< 75 μg) macroinvertebrates as well (i.e. 502 versus 271–386/m^3). This concordance between ODI relationships and macroinvertebrate drift suggested an optimal-diet response by darters.

One way to examine the sensitivity of prey-size relationships to ecotopic variation in macroinvertebrate abundance was to compare *P. nigrofasciata* from the two sites showing the widest difference in drift flux. The most upstream site on Perkins Creek displayed the lowest drift flux (i.e. 37/m^3), and a mid-stream site on Black Creek (New Bridge) showed the highest drift flux (i.e. 614/m^3). Although drifting chironomid larvae were almost twice as abundant at the Perkins Creek site (i.e. 14.3 versus 7.9/m^3), all other types of drifting macroinvertebrates were much more abundant at the New Bridge site (i.e. 606 versus 23/m^3). Furthermore, all sizes of macroinvertebrates were considerably more abundant at the New Bridge site than at Perkins Creek (Fig. 5A). Perhaps reflecting the extremely low macroinvertebrate abundance, Perkins Creek *P. nigrofasciata* was the only sample of this species with both nonsignificant maximum and minimum prey-size relationships.

Despite extremely different drift levels, distributions of ODI data were similar at the two sites (Fig. 5B). Perkins Creek *P. nigrofasciata* showed a definte ontogenetic ODI relationship, even though macroinvertebrate abundance was so low. Furthermore, large darters did not display particularly high ODI values from diet expansion at Perkins Creek. Perhaps the extremely low abundance of all macroinvertebrates, including small sizes, precluded the expression of particularly high ODI values at Perkins Creek.

Discussion

Ontogenetic Significance

Past feeding studies of *Hadropterus* differ as to whether prey size is important. Mathur (1973) suggested that *P. nigrofasciata*

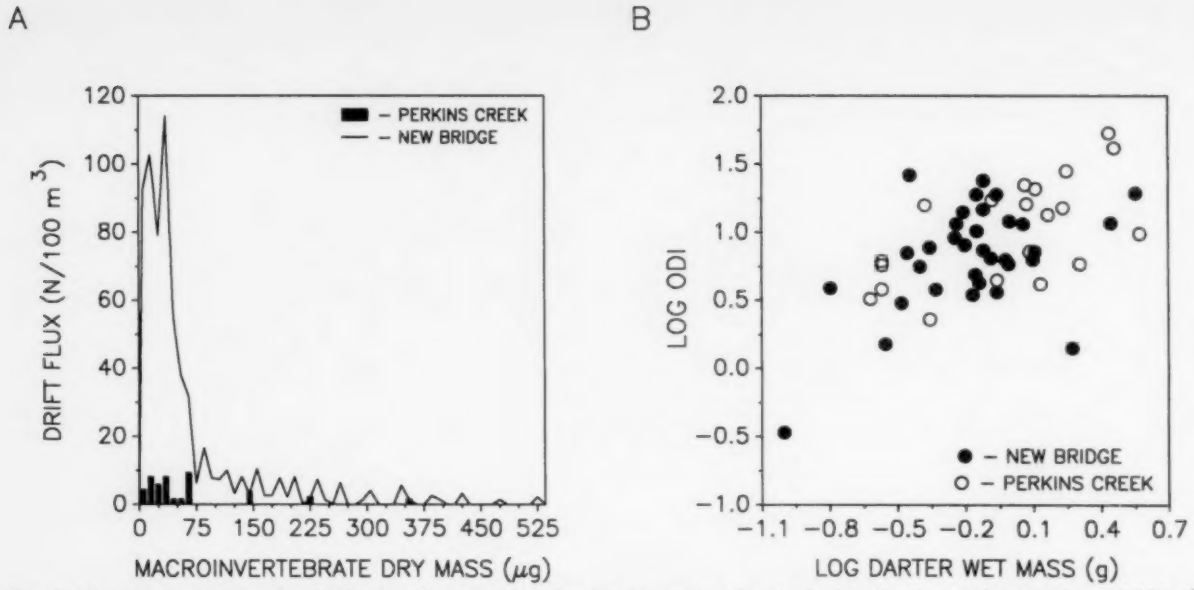

FIG. 5. (A) Macroinvertebrate size distributions from two sites showing the greatest disparity in drift flux (i.e. Perkins Creek = 37/100 m^3; New Bridge = 614/100 m^3); (B) overlaid ODI data for *P. nigrofasciata* from the two sites showing the greatest disparity in macroinvertebrate drift.

were not prey-size selective because large darters ingest small dipterans. However, Miller (1983) found a definite ontogenetic prey-size relationship for *P. sciera*, although it is unclear whether ontogenetic change in prey size reflected gape limitation or prey-size selection. In this study, prey size increased with darter size for all three *Hadropterus* species. Furthermore, decelerating ODI curves indicated that ontogenetic increases in prey-size use reflected prey-size selection.

However, ODI curves also showed that diets were increasingly less optimal with increasing darter size. Geometrically decreasing abundances of progressively larger prey must have required large darters to have less optimal diets than small darters could achieve. High abundances of small prey rather than prey-size selection presumably resulted in more optimal diets for small darters. If small darters were being prey-size selective, ODI curves initially would have ascended more slowly. Provided all prey were eaten as encountered and assuming a modal prey size (i.e. 0.56 μg dry weight chironomid larva), a darter would have to be as small as 0.032 g wet mass (i.e. 15.2 mm SL) to achieve an optimal diet. This is even smaller than an adult of the smallest derived species, *Etheostoma fonticola*, which reaches an adult size of 35.5 mm SL (Page 1983).

Although diets were progressively less optimal with increasing darter size, there still was a general ontogenetic shift in feeding tactics, from number maximizing to prey-size selection. Assuming a lognormal distribution of available prey sizes, slopes of ODI curves should have approached 1 in value, if darters of all sizes indiscriminately consumed all sizes of prey. Instead, slopes were considerably lower than 1, even when the ODI relationship included darters as large as 45 g wet weight (i.e. large *P. lenticula*). Although they showed ontogenetic diet shifts, all sizes of darters relied on the same lotic prey-size spectrum. This may explain why the upper size limit of darters is roughly 50 g and why *P. lenticula* is somewhat rare. Indeed, population estimates at my study sites indicated roughly one *P. lenticula* to 100 other *Hadropterus* (Rakocinski 1986). However, *P. lenticula* is probably more abundant downstream, in rivers (Page 1983 and pers. obs.), where large prey also may be more abundant.

The optimum prey size of *P. nigrofasciata* conformed closely with the maximum prey size, rather than agreeing with the mean prey size, as Kislalioglu and Gibson (1976) found for the 15-spined stickleback (*Spinachia spinachia*). The slope of the maximum prey-size relationship for *P. nigrofasciata* was essentially 1, showing a constant proportionality between darter size and maximum prey size. As indicated by the hairpin-shaped hypothetical ODI curve, gape limitation should preclude darters from eating prey that are much larger than the optimum size. Thus, the constant proportionality expressed in the maximum prey-size relationship also reflected that of the optimum prey size.

Prey-size use by darters is presumably related to their rates of growth and survival. Optimal foraging theory predicts that an efficient prey-size relationship should provide rapid acquisition of prey mass and/or reduced foraging time (Schoener 1971). For small darters, time spent foraging probably corresponds directly with exposure to predation. Moreover, relative prey size has been shown to be directly related to growth efficiency and scope for growth for particulate-feeding fishes (Paloheimo and Dickie 1966; Kerr 1971; Wankowski and Thorpe 1979). Rapid growth as a result of an efficient prey-size relationship also would confer a kind of predation refuge. Small darters must be afforded good scope for growth by their more efficient prey-size relationship. Furthermore, through ontogenetic prey-size selection, large darters can apparently sustain a positive scope for growth up to sizes as large as 50 g wet weight.

The marked ontogenetic response in prey-size use shown by darters may be a product of their coevolution with prey. An ontogenetic response was repeated across both species and sites,

appearing like an intrinsic characteristic of the fish populations. Historically, the lognormal lotic prey-size distribution has exerted a persistent selection pressure on predators. Page and Swofford (1984) even proposed that lotic prey-size distributions were largely responsible for the evolutionary trend toward smaller body sizes in darters. The fact that primitive darters grow very large at the expense of having less optimal diets demonstrates that other forces have effectively opposed the effects of prey-size distributions on body-size reduction. Such benefits of being large include hydrodynamic, competitive, and predation refuge advantages (Page and Swofford 1984).

One way large darters can respond adaptively to the prey-size spectrum is for them to develop a behavioral tactic of active prey-size selection. Griffiths (1975) hypothesized that an ontogenetic shift from number maximizing to prey-size selection requires learning. Wide individual variation in ODI values both within and across darter sizes suggests that learning could have effected a gradual transition in feeding tactics. Active prey-size selection through bypassing of small prey is a likely mechanism of prey use for large darters. There are perceptual and mechanical limits that bracket the range of relative prey sizes fish can consume (cf. Wankowski and Thorpe 1979). These limits should define the range of prey sizes that may be passively selected. However, lower prey-size limits appeared to be similar between small and large darters, since even large darters ingested some small prey (cf. Mathur 1973).

Although darter ODI relationships increased monotonically, other forms of ODI relationships are also possible for particulate feeders. Ross (1978) found an interesting U-shaped ontogenetic curve of relative prey-size use for leopard searobins (*Prionotus scitulus*). Thus, the ODI relationship for the leopard searobin might be hump-shaped, first diverging to a peak and then decreasing with increasing fish size. Quadratic ODI relationships might often occur in marine systems which have multiple prey-size spectra (Pearre 1986). Also, the relatively large mouth size of searobins may allow them to shift across different prey-size spectra as they grow.

Previous feeding studies of *Percina* have noted distinct ontogenetic changes in prey-type use. Upon reviewing 48 darter feeding studies, Page (1983) described two major ontogenetic prey-type shifts that further suggest concomitant shifts in prey-size use. The first shift is from microcrustaceans to small macroinvertebrates, and the second shift is from small to large macroinvertebrates. He concluded that large darters generally display richer diets of larger food items than small darters. In addition to darters, Grossman (1980) found that ontogenetic changes in prey type also were linked to changes in prey-size use by bay goby (*Lepidogobius lepidus*).

Interspecific Significance

Diets of syntopic *P. nigrofasciata* and *P. sciera* differed in ways that characterized relatively prey-size selective and number-maximizing feeding tactics, respectively. Compared with large *P. sciera*, the diet of large *P. nigrofasciata* was broader and consisted of fewer, but larger prey. These dietary differences also were reflected in slopes of ODI relationships, with a lower slope demonstrating a more optimal diet for large *P. nigrofasicata*. Such differences in feeding tactics may help explain why *P. nigrofasciata* always reaches larger sizes where both species are syntopic (Rakocinski 1986).

Although *P. nigrofasciata* developed a stronger prey-size selective response than *P. sciera*, juveniles of both darter species were number maximizers. This was shown by ODI curves that initially ascended rapidly for both species. However, juveniles of the two darter species concentrated on different prey types, such as chironomid larvae or simuliid larvae. Thus, feeding tactics were really different between all sizes of these two species. The extent to which interspecific interactions affected the expression of different feeding tactics remains unknown. At any rate, interspecific variation in feeding tactics among these primitive darters showed how derived darters could have evolved unique feeding tactics.

Feeding tactics of primitive darters can be understood as an interplay between prey-type and prey-size selection. A strong ontogenetic tactic of prey-size selection, like that shown by *P. nigrofasciata*, apparently required large darters to broaden their diets to include a wider array of large prey types. One possible trade-off of this kind of diet response in a complex environment, like a stream, is that large prey are added to the diet at the expense of decreased prey-capture success (Persson 1985). This trade-off could result from lower training bias as the diet is broadened to include less familiar prey types (Dill 1983).

Indeed, the feeding behavior of darters at two sites, Tallahala Creek and Cypress Creek Landing, suggested that *P. sciera* may experience greater prey-capture success than *P. nigrofasciata* (Rakocinski 1986). Despite wide differences in numbers of prey ingested between darter species at Cypress Creek Landing, feeding rates were virtually identical between species, ranging between 2.03 ± 0.33 and 2.27 ± 0.38 bites/min (mean $\pm$ SD). Thus, unless *P. nigrofasciata* evacuated prey faster than *P. sciera*, the latter species either experienced better prey-capture success and/or spent more time foraging than *P. nigrofasciata* at Cypress Creek Landing.

Diet variation also may have resulted from differences in feeding substrate use (e.g. gravel, sand, submerged debris). Current velocities associated with various feeding substrates were correlated with the mean number of prey ingested at two sites ($P < 0.05$) (Rakocinski 1986). This suggested that prey-capture success may have been related to feeding substrate use in conjunction with ambient current velocity. Moreover, each darter species actually specialized on different prey types, since there was greater interspecific overlap (α) in feeding substrate than in diet at Cypress Creek Landing (i.e. p_i based on numbers of prey) (0.76 substrate versus 0.42 diet).

Often, interspecific differences in prey-size use appear as the outcome of different feeding modes. For example, prey-size differences among surfperches result from contrasting feeding modes of winnowing and visual picking (Schmitt and Coyer 1982). Although the darter species used the same active feeding mode involving particulate invertivorous feeding, their feeding tactics still differed.

Ecotopic Significance

Among the four Black Creek sites, ODI relationships of *P. nigrofasciata* varied in a manner consistent with optimal-diet theory. Adjusted means of ODI relationships were lowest from two of the sites with high relative abundances of large drifting macroinvertebrates (i.e. >7.5 μg dry weight), and the site with the lowest adjusted mean ODI had the highest abundances of both small and large drifting macroinvertebrates. This agrees with optimal-diet theory because diets were more optimal where valuable prey (i.e. large macroinvertebrates) were

abundant, regardless of the abundance of less-valuable prey (i.e. small macroinvertebrates) (Pyke 1984).

However, the conclusion that darters showed an ecotopic optimal-diet response must remain tentative. Three samples of *P. nigrofasciata* from sites outside Black Creek also had low adjusted ODI means. Two of these samples had narrow size ranges of larger darters and were excluded from further consideration because they had nonsignificant ODI relationships. Moreover, the consistency between drift flux and adjusted ODI means might have diminished if all these samples could have been included in an ANCOVA.

Although the third outside sample from Perkins Creek did show a significant ODI relationship, drift samples from this site yielded extremely low abundances of all sizes of macroinvertebrates. Nonsignificant maximum and minimum prey-size relationships at this site implied that a fairly even distribution of prey sizes was used by darters of all sizes. The low abundance of small macroinvertebrates at Perkins Creek probably precluded the expression of higher ODI values. Consequently, ODI data were similar between this site and the site that showed the highest abundances of both small and large macroinvertebrates.

Optimal-diet responses in relation to prey abundance have been shown for planktivorous and benthic fishes in lentic systems (Werner and Hall 1974; Mittelbach 1981b; Bartell 1982). However, optimal-diet responses have not been well documented for benthic stream fishes (Gatz 1983). Because plankton abundance can be directly measured, selection indices that directly incorporate prey availability are useful for studies of planktivorous fish. However, it is very difficult to accurately measure prey availability for benthic predators in heterogeneous lotic habitats. In this study, drift rates of lotic macroinvertebrates were used as a reflection of variation in relative prey abundance among sites. In conjunction with this approximate measure, the ODI proved to be useful for recognizing prey selection in a lotic system. If prey availability were accurately measured and used to generate expected ODI relationships under a null hypothesis of no prey selection, the ODI approach could prove to be even more insightful.

Schluter (1981) questioned whether optimal foraging theory could be applied in complex habitats, like those of streams, and Gatz (1983) questioned whether fishes could forage optimally in streams, where levels of food resources are low. This study demonstrated that optimal foraging theory could be used to understand the feeding tactics of benthic stream fishes. Although primitive darters did not have optimal diets, optimal foraging principles helped to elucidate patterns of prey-size use and feeding tactics of darters.

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Vertical Size–Depth Distribution Properties of Midwater Fish off Bermuda, with Comparative Reviews for Other Open Ocean Areas

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Brooks, A. L., and R. A. Saenger. 1991. Vertical size–depth distribution properties of midwater fish off Bermuda, with comparative reviews for other open ocean areas. Can. J. Fish. Aquat. Sci. 48: 694–721.

The nighttime (N) and daytime (D) size–depth distributions of mesopelagic fish at Ocean Acre, a typical deepwater site in the North Sargasso Sea, are described using archival discrete-depth data from the surface to about 1500 m. The N/D abundance distributions $n(z)$ for a representative group of 18 swimbladdered species indicate that fish are concentrated in the 0–150 m euphotic zone at night and in the 400–1000 m zone during the day in spring, summer, and winter. Seasonal succession in the average life stage size classes of the bladdered group occurs, but all classes are present year-round due to the variety of specific spawning patterns. The noncoincident N/D depth niches of individual bladdered species apparently are organized to reduce competition. Normalized N/D depth distributions $\hat{n}(z)$ for the bladdered group are similar throughout the year, and appear to be determined, respectively, by the N distribution of zooplankton biomass and the D underwater light field, other hydrographic variables having little direct influence. Also, it seems likely that the form of $\hat{n}(z)$ is relatively insensitive to species composition for such groups. These hypotheses are verified qualitatively by comparing specific and group distribution properties at other ocean sites with those at Ocean Acre.

Les répartitions longueur–profondeur nocturne (N) et diurne (D) des poissons mésopélagiques à Ocean Acre, une zone profonde typique de la mer des Sargasses nord, sont décrites à partir de données d'archives sur les profondeurs discrètes à partir de la surface jusqu'à environ 1 500 m. Les distributions $n(z)$ de l'abondance N/D d'un groupe représentatif de 18 espèces de poissons à vessie natatoire révèlent qu'ils sont concentrés dans la zone trophogène (1–150 m) pendant la nuit et dans la zone s'étendant de 400 à 1 000 m pendant le jour au cours du printemps, de l'été et de l'hiver. Il se produit une succession saisonnière des classes de taille moyennes de poissons à vessie natatoire, mais toutes les classes sont présentes pendant l'année à cause de la diversité des régimes de reproduction. Les niches de profondeur N/D non coïncidentes de chaque espèce de poissons à vessie natatoire sont, de toute apparence, disposées de façon à réduire la compétition. Les distributions normalisées $\hat{n}(z)$ des profondeurs N/D du groupe de poissons à vessie natatoire sont semblables pendant toute l'année et semblent être déterminées par la distribution N de la biomasse zooplanctonique et le champ lumineux sous-marin (D), respectivement; d'autres variables hydrographiques semblent avoir peu l'influence directe. De plus, il semble probable que la forme de $\hat{n}(z)$ soit relativement insensible à la composition spécifique dans le cas de ces groupes. Les hypothèses formulées sont vérifiées qualitativement par comparaison des caractéristiques des espèces et de la distribution des groupes dans d'autres zones océaniques.

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Ocean Acre (OA) is a comprehensive research program undertaken jointly by the Smithsonian Institution, the University of Rhode Island, the Naval Underwater Systems Center (NUSC), and the Naval Oceanographic Office to study the biological and acoustical characteristics of an open ocean ecosystem (Brown 1968; Anonymous 1970; Gibbs and Roper 1971; and Brown 1976). Detailed trawl-based studies of the faunal composition, vertical distribution, and various aspects of the life histories and ecology of the four individual fish families which dominate the mesopelagic community in waters off Bermuda were reported by Bond (1974) (Gonostomatidae), Gibbs et al. (1971a) (Myctophidae), Howell (1975) (Sternoptychidae), Karnella (1983) (Myctophidae), and Keene (1970) (Melamphaidae). A general description of the depth distributions and diel vertical migration of these four families and of the cephalopods were given by Gibbs and Roper (1971) for the first seven of the 14 cruises made to the sample site. In a more recent account, Gibbs and Krueger (1987) presented a comprehensive compilation of the biology of the midwater fishes belonging to the Sternoptychidae, Myctophidae, and Melamphaidae captured off Bermuda.

The present investigation of Ocean Acre midwater fish is designed to support the development of size–depth distribution models of swimbladdered fish needed for bioacoustic prediction at low frequencies, so the approach and emphasis are different from the studies mentioned above. Acoustic volume scattering in the ocean up to about 20 kHz is caused predominantly by resonance scattering from the gas-filled swimbladders of numerous mesopelagic fish species found in sound-scattering layers (Farquhar 1971; Andersen and Zuhuranec 1977). Above 20 kHz, geometric scattering contributions from both bladdered and nonbladdered fish and zooplankton become increasingly important. To predict volume-scattering strength $S(z,f)$ as a function of depth z and frequency f for frequencies up to 50 kHz, say, the vertical size–depth distributions of both fish species groups must be known. Ideally, each distribution would be expressed in the form of a two-dimensional density distribution $n(l,z)$ during daytime (D) and nighttime (N) periods,

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where z is depth and l is fish standard length. Here we are primarily concerned with the swimbladdered species group and its principal constituent species. This group is believed to account for the low-frequency volume reverberation observed at Ocean Acre below 20 kHz (Fisch and Dullea 1973; Fisch 1977; Brooks and Brown 1977).

From the standpoint of bioacoustic prediction, the distribution properties of individual species are of interest primarily for the insight they give into the distribution properties of their respective scattering groups. Bioacoustic considerations provide still another reason for focusing attention on species groups. Scattering layers in different ocean areas have many common features, as revealed by surveys with precision depth recorders operating around 10 kHz and low-frequency volume-scattering strength profile measurements. This suggests that the distributions and acoustic characteristics of bladdered species groups in these layers may be rather similar and not very sensitive to species composition.

Models of $n(l,z)$ that include environmental factors have not been developed for bioacoustic applications for several reasons. Because of the small volumes of water that can be sampled in practice, and the many limitations of discrete-depth sampling gear (Pearcy 1983), there are serious gaps and ambiguities in all biological trawl data. A more fundamental reason is the lack of physical understanding of the relation between $n(l,z)$ and the environment. It is generally accepted that underwater light intensity triggers diel vertical migration and that nighttime distributions of mesopelagic fish are closely related to the distribution of zooplankton. But to what extent are physiologically important hydrographic variables such as temperature $T(z)$, salinity $S(z)$, oxygen $O_2(z)$, and hydrostatic pressure $P(z)$ responsible for the particular form of $n(l,z)$ in a given faunal area? Knowledge of the relation of size–depth distribution properties of bladdered fish species groups to the biological and physical environment is essential for future model development. We discuss this difficult question by comparing fish distribution and environmental properties at OA with those in other ocean areas. As will be shown, in speciose open ocean areas, say, from 10°N to 40°N, a number of prominent features of N/D distributions $n(l,z)$ can be expected to be similar and relatively independent of species composition and hydrographic properties. These more general considerations are deferred to the Discussion section. In the Results section, we describe the seasonal size–depth properties of mesopelagic fish at OA, particularly those of the swimbladdered species group and its 18 principal constituent species.

Materials and Methods

Biological Sampling

During the 5-yr period from October 1967 to June 1972, 14 experiments were performed at the OA site, a 1° quadrangle centered at 32°N, 64°W. More than 300 fish species from 80 families were collected. Approximately 90% of these specimens belong to the four families Myctophidae, Gonostomatidae, Sternoptychidae, and Melamphaidae (Brown and Brooks 1974). With the exception of adults of the genus *Cyclothone* (Gonostomatidae), most of the midwater fish fauna possess a gas-filled swimbladder and can thus be expected to contribute to sound scattering in the sea (Marshall 1951, 1960). The distribution of trawl samples by cruise number and dates and the participating research vessels are given in Brown and Brooks (1974) and Gibbs and Karnella (1987).

Data examined in this paper include neuston and Isaacs–Kidd Midwater Trawl (IKMT) discrete-depth day and night samples collected only during OA cruises 10 (29 May – 11 June 1970), 12 (22 August – 8 September 1971), 13 (22 February – 3 March 1972), and 14 (4 – 12 June 1972). These cruises were selected because they included the spring (OA 10 and 14), summer (OA 12), and winter (OA 13) seasons, furnished large numbers of discrete-depth samples, and provided a more complete depth coverage of the water column than any other cruises. During these four cruises, thousands of midwater fish specimens were captured during a total of 317 h of discrete-depth towing (Table 1). The 383 trawl samples obtained represent almost 80% of the total number of 3-m IKMT discrete-depth trawl samples taken during all 14 OA experiments. Day and night are here defined as the periods between 1.5 h after sunrise to 1.5 h before sunset (day) and 1.5 h after sunset to 1.5 h before sunrise (night). This effectively eliminates samples collected during the daily migration periods.

Neuston samples were taken with a 1-m ring net with a mesh aperture of about 0.75 mm. This net was set so that the mouth was half submerged and towed alongside the ship 2–3 m outboard of the hull. At night, specimens were collected from the net at 0.5 h intervals and the net returned to the water. During the day, the duration of each tow was usually 1 h.

All other discrete-depth sampling during cruises 10, 12, 13, and 14 was done with a 3-m IKMT with the same basic design as described by Isaacs and Kidd (1953) and described in specific detail by Brooks et al. (1974). The principal dimensions of bridle and paravane were as specified for the 3-m IKMT in Aron (1962). The net cod end consisted of a six-inch (15.2-cm) diameter, four-chambered sampler described by Aron et al. (1964). Modifications to the electronics of this original sampler were made by Giuliano and Battista (1971) which greatly improved its reliability. The IKMT is estimated to be most efficient in capturing fish with lengths between 10 and 50 mm (Gibbs and Karnella 1987).

All net tows were made at a ship speed of between 3 and 4 knots (kn). Net depth, water temperature at depth, and net speed (all variables not available on all cruises) relayed up the electromechanical tow cable from sensors in the IKMT net instrument package allowed continuous onboard monitoring of these parameters. The usual sampling procedure was to shoot the net with all four chamber doors cocked open, allowing all animals to pass through freely. After adjusting the net to the desired depth the rearmost door was closed by an onboard command signal, thereby forming the first sampling chamber. Each subsequent signal released the door immediately forward creating the second and third discrete-depth sampling chambers. Ordinarily, 1-h-long samples from a single prescribed depth were collected in each of the three chambers. A final, nondiscrete-depth, oblique sample was collected in the fourth chamber as the trawl was raised to the surface. This sampling regimen reduced the potential for contamination of the three repetitive discrete-depth samples with specimens from other depths. For a more detailed discussion of these procedures and sample processing methods, the reader is referred to Roper et al. (1970), Gibbs et al. (1971b), Brown and Brooks (1974), and Gibbs and Karnella (1987).

Faunal Composition of the Data Base

On the basis of trawl samples obtained in the major OA experiments and swimbladder size measurements made by

TABLE 1. Numbers of hours of neuston and IKMT towing within each discrete-depth interval for nighttime (1.5 h after sunset to 1.5 h before sunrise) and daytime (1.5 h after sunrise to 1.5 h before sunset) periods.

Nominal depth (m)	Depth interval (m)	Spring				Summer, OA12		Winter, OA 13		Total hours at depth
		OA 10		OA 14						
		Night	Day	Night	Day	Night	Day	Night	Day	
0	0–1	6.2	5.7	3.8	2.9	1.7	1.4	7.3	1.1	30.1
25	1–50	1.0	—	0.5	1.5	2.0	2.0	6.4	2.5	15.9
75	51–100	3.0	3.0	1.5	4.7	—	—	8.0	1.8	22.0
125	101–150	1.0	—	1.5	3.0	3.0	—	3.5	2.3	14.3
175	151–200	—	6.0	1.7	3.0	3.0	—	3.0	1.9	18.6
225	201–250	3.0	—	—	—	3.0	—	3.0	—	9.0
275	251–300	—	3.0	2.2	3.0	3.0	—	—	—	11.2
325	301–350	—	—	—	3.0	3.0	—	1.9	1.5	9.4
375	351–400	1.0	3.0	2.5	3.0	2.0	—	3.2	2.2	16.9
425	401–450	2.0	—	—	—	3.0	1.0	3.0	—	9.0
475	451–500	—	1.0	3.0	2.0	3.0	2.0	2.5	2.0	15.5
525	501–550	3.0	—	—	—	—	3.0	3.0	—	9.0
575	551–600	2.0	—	2.4	3.0	—	3.0	2.0	2.2	14.6
625	601–650	—	3.0	—	—	1.0	3.0	1.0	—	8.0
675	651–700	—	3.0	—	3.0	2.0	—	—	—	8.0
725	701–750	—	—	—	—	2.0	3.0	3.0	2.5	10.5
775	751–800	—	2.0	1.6	3.0	3.0	3.0	3.0	—	15.6
825	801–850	2.0	—	—	—	—	3.0	—	3.0	8.0
875	851–900	—	—	—	3.0	3.0	—	—	—	6.0
925	901–950	—	—	—	—	3.0	3.0	—	—	6.0
975	951–1000	—	2.0	3.0	2.5	3.0	—	1.0	—	11.5
1025	1001–1050	—	—	—	—	—	3.0	2.0	2.5	7.5
1075	1051–1100	1.0	1.0	—	—	—	—	—	—	2.0
1125	1101–1150	—	1.0	—	—	—	3.0	—	—	4.0
1175	1151–1200	—	1.0	—	—	—	2.0	—	—	3.0
1225	1201–1250	—	—	3.0	3.0	1.0	1.0	1.0	1.0	10.0
1275	1251–1300	—	—	—	—	2.0	1.0	2.0	1.9	6.9
1325	1301–1350	—	—	—	—	—	2.0	—	—	2.0
1375	1351–1400	—	—	—	—	—	—	—	—	0.0
1425	1401–1450	—	—	—	—	—	—	—	—	0.0
1475	1451–1500	—	—	—	—	—	1.0	—	—	1.0
1525	1501–1550	—	—	—	3.0	—	2.0	3.3	3.2	11.5
Total hours		25.2	34.7	26.7	46.6	46.7	42.4	63.1	31.6	317.0

Kleckner and Gibbs (1972) and Kleckner (1974, and unpubl. data), Brown and Brooks (1974) identified 55 swimbladdered taxa as the predominant contributors to low-frequency acoustic scattering at OA. These taxa represented virtually all the OA fishes known at that time to possess a gas-filled swimbladder. At our request, the Smithsonian Institution provided discrete-depth daytime and nighttime size–depth information for this bladdered group and for each of its constituent species for OA 10, 12, 13, and 14. In these four experiments, only 53 of the 55 bladdered taxa were found in the discrete-depth samples (Table 2). A high proportion of the 53 swimbladdered taxa are represented by only a few specimens. To facilitate detailed analysis of group distribution properties, a representative group of numerically dominant taxa was selected ("selected predominant species" (SPS), asterisked in Table 2). They were obtained by first summing the number per hour of each of the 53 swimbladdered taxa captured in nighttime, discrete-depth IKMT and neuston samples collected during OA cruises 12, 13, and 14. Corresponding sums were also calculated for daytime samples. These three cruises were chosen because they covered the summer, winter, and spring season and because of their extensive depth coverage. All taxa with a nighttime or daytime number per hour figure of at least 2% of the corresponding number per hour for all 53 taxa in at least one of the three cruises were included.

Swimbladdered fishes were divided into "larvae–postlarvae" (≤13 mm), "juveniles" (14–22 mm), "subadults" (23–33 mm), and "adults" (≥34 mm) using detailed life stage size–range information for the 18 individual SPS given by Keene (1970), Krueger (1972), Krueger and Bond (1972), Bond (1974), Howell (1975), and Karnella (1983). The boundaries between the various nominal life stage size classes were determined as follows. Minimum and maximum lengths for the different stages of individual species were averaged for the 18 species. The cut point between adjacent stages was taken as the midpoint between the average maximum for the earlier stage and the average minimum for the later stage.

Similar discrete-depth data were provided by the Smithsonian Institution for the nonbladdered taxa group, defined as all mesopelagic fish taxa found at OA other than the 55 predominant swimbladdered taxa. Depth distribution properties of individual nonbladdered taxa are not considered in this paper and we shall be content here simply with listing the overall numbers of predominant nonbladdered taxa caught in OA 12, 13, and

TABLE 2. Swimbladdered fish taxa principally responsible for low-frequency volume scattering at OA (Brown and Brooks 1974) captured in discrete-depth IKMT and neuston net trawls in OA 10, 14, 12, and 13. Absolute number and number per hour (in italics) are tabulated for nighttime (N) and daytime (D) periods. The 18 SPS are indicated by an asterisk (see text).

	Spring										
	OA10		OA14		Summer, OA 12		Winter, OA 13		Total		Combined total
Mesopelagic fish taxa	N	D	N	D	N	D	N	D	N	D	N + D
1. *Anoplogaster cornuta*	—	—	—	3	6	2	1	—	7	5	12
	—	—	—	*1.1*	*2.0*	*0.7*	*0.2*	—	*2.2*	*1.8*	*4.0*
2. *Argyropelecus aculeatus*	—	4	20	19	47	16	37	20	104	59	163
	—	*1.8*	*8.2*	*6.4*	*17.5*	*7.5*	*16.4*	*11.2*	*42.1*	*25.1*	*67.2*
3. *Argyropelecus hemigymnus**	6	19	52	68	114	131	83	49	255	267	522
	3.2	*6.9*	*20.6*	*22.6*	*42.5*	*52.5*	*33.8*	*23.4*	*96.9*	*98.5*	*195.4*
4. *Benthosema suborbitale**	1	6	1	3	129	4	7	14	138	27	165
	1.0	*2.0*	*0.6*	*1.0*	*69.3*	*1.3*	*0.8*	*6.1*	*70.7*	*8.4*	*79.1*
5. *Bolinichthys indicus**	42	4	14	7	93	206	228	140	377	357	734
	14.0	*1.3*	*9.1*	*2.3*	*33.9*	*78.2*	*38.6*	*60.3*	*81.6*	*140.8*	*222.4*
6. *Bolinichthys photothorax*	—	—	—	*1*	*1*	—	*1*	—	2	*1*	*3*
	—	—	—	*0.5*	*0.3*	—	*0.3*	—	*0.6*	*0.5*	*1.1*
7. *Bonapartia pedaliota**	22	6	64	5	89	1	113	7	288	19	307
	13.7	1.8	26.4	2.0	31.6	0.3	41.9	3.4	99.9	5.7	105.6
8. *Bregmaceros sp.*	—	—	1	—	5	—	2	1	8	1	9
	—	—	*0.6*	—	*2.0*	—	*0.4*	*0.5*	*3.0*	*0.5*	*3.5*
9. *Ceratoscopelus maderensis*	—	—	1	1	5	18	—	—	6	19	25
	—	—	*2.0*	*0.3*	*2.0*	*6.3*	—	—	*4.0*	*6.6*	*10.6*
10. *Ceratoscopelus warmingi**	17	8	47	—	51	48	172	36	287	92	379
	14.3	*6.5*	*36.3*	—	*21.0*	*16.7*	*29.1*	*18.5*	*86.4*	*35.2*	*121.6*
11. *Diaphus brachycephalus*	8	—	1	—	1	—	—	1	10	1	11
	4.7	—	*0.6*	—	*0.3*	—	—	*0.4*	*0.9*	*0.4*	*1.3*
12. *Diaphus metapoclampus*	1	13	3	1	—	—	19	8	23	22	45
	0.5	*4.3*	*1.2*	*0.3*	—	—	*7.2*	*3.1*	*8.4*	*3.4*	*11.8*
13. *Diaphus mollis*	37	4	4	7	32	56	61	8	134	75	209
	15.7	*2.7*	*2.7*	*2.3*	*14.3*	*19.0*	*12.9*	*4.0*	*29.9*	*25.3*	*55.2*
14. *Diaphus problematicus*	2	—	—	—	—	1	—	—	2	1	3
	1.3	—	—	—	—	*0.3*	—	—	*1.3*	*0.3*	*1.6*
15. *Diaphus rafinesquei*	24	7	13	1	1	3	28	7	66	18	84
	8.0	*3.0*	*4.9*	*0.3*	*0.3*	*1.0*	*6.7*	*3.5*	*11.9*	*4.8*	*16.7*
16. *Diogenichthys atlanticus**	53	44	78	98	86	111	174	82	391	335	726
	25.8	*20.5*	*52.3*	*31.2*	*31.8*	*38.8*	*28.5*	*34.0*	*112.6*	*104.0*	*216.6*
17. *Hygophum benoiti**	1	3	15	17	447	114	463	61	926	195	1121
	0.3	*1.5*	*8.9*	*5.0*	*184.7*	*40.4*	*75.4*	*24.4*	*269.0*	*69.8*	*338.8*
18. *Hygophum hygomi**	7	40	2	6	—	4	178	108	187	158	345
	5.5	*15.0*	*0.6*	*2.0*	—	*1.3*	*37.5*	*44.7*	*38.1*	*48.0*	*86.1*
19. *Hygophum taaningi*	—	—	2	2	3	—	2	—	7	2	9
	—	—	*0.7*	*0.8*	*1.2*	—	*0.3*	—	*2.2*	*0.8*	*3.0*
20. *Ichthyococcus ovatus*	5	2	7	36	17	15	27	15	56	68	124
	3.7	*0.6*	*3.0*	*12.4*	*6.0*	*5.3*	*11.1*	*7.5*	*20.1*	*25.2*	*45.3*
21. *Lampadena chavesi*	2	5	7	5	3	—	1	—	13	10	23
	1.3	*1.7*	*4.7*	*1.6*	*1.0*	—	*0.8*	—	*6.5*	*1.6*	*8.1*
22. *Lampadena speculigera*	4	8	5	1	—	3	17	10	26	22	48
	1.5	*4.0*	*2.7*	*0.3*	—	*1.3*	*3.6*	*4.1*	*6.3*	*5.7*	*12.0*
23. *Lampadena urophaos*	9	—	—	—	1	1	3	1	13	2	15
	3.7	—	—	—	*0.3*	*0.3*	*0.7*	*0.4*	*1.0*	*0.7*	*1.7*
24. *Lampanyctus alatus*	4	—	1	—	—	1	—	3	5	4	9
	1.3	—	*0.5*	—	—	*0.3*	—	*1.1*	*0.5*	*1.4*	*1.9*
25. *Lampanyctus ater*	22	16	8	10	12	10	11	38	53	74	127
	8.2	*11.5*	*4.5*	*3.0*	*5.0*	*5.3*	*3.2*	*13.4*	*12.7*	*21.7*	*34.4*
26. *Lampanyctus crocodilus*	5	16	8	10	11	4	1	1	25	31	56
	2.5	*8.0*	*7.7*	*2.8*	*2.8*	*0.5*	*0.3*	*0.3*	*10.8*	*3.6*	*14.4*
27. *Lampanyctus cuprarius**	37	36	12	42	37	22	67	49	153	149	302
	15.8	*24.0*	*5.7*	*13.1*	*14.0*	*8.0*	*25.0*	*17.7*	*44.7*	*38.8*	*83.5*
28. *Lampanyctus festivus*	7	—	3	9	8	17	28	22	46	48	94
	2.3	—	*1.7*	*2.3*	*2.6*	*5.7*	*6.4*	*9.0*	*10.7*	*17.0*	*27.7*
29. *Lampanyctus lineatus*	—	1	2	1	—	—	2	2	4	4	8
	—	*1.0*	*0.8*	*0.3*	—	—	*0.8*	*0.3*	*1.6*	*0.6*	*2.2*
30. *Lampanyctus photonotus*	1	2	9	9	15	3	120	22	145	36	181
	0.3	*1.5*	*7.3*	*3.2*	*6.2*	*2.7*	*29.1*	*7.8*	*42.6*	*13.7*	*56.3*

TABLE 2. (*Concluded*)

Mesopelagic fish taxa	Spring OA10 N	Spring OA10 D	Spring OA14 N	Spring OA14 D	Summer, OA 12 N	Summer, OA 12 D	Winter, OA 13 N	Winter, OA 13 D	Total N	Total D	Combined total N + D
31. *Lampanyctus pusillus**	48	178	76	161	150	360	109	92	383	791	1174
	22.3	*61.8*	*50.6*	*53.9*	*63.5*	*130.7*	*25.3*	*39.9*	*139.4*	*224.5*	*363.9*
32. *Lepidophanes gaussi**	3	13	3	8	98	2	6	11	110	34	144
	1.0	*5.3*	*3.3*	*2.7*	*52.3*	*1.0*	*0.9*	*3.8*	*56.5*	*7.5*	*64.0*
33. *Lepidophanes guentheri*	—	—	2	2	6	3	1	4	9	9	18
	—	—	*2.7*	*0.5*	*1.7*	*1.2*	*0.2*	*1.4*	*4.6*	*3.1*	*7.7*
34. *Lobianchia dofleini**	96	30	42	9	40	50	24	16	202	105	307
	63.3	*13.9*	*42.7*	*3.9*	*14.3*	*16.7*	*5.5*	*7.7*	*62.5*	*28.3*	*90.8*
35. *Lobianchia gemellari*	17	16	4	9	2	—	24	16	47	41	88
	7.7	*5.5*	*2.0*	*3.9*	*0.7*	—	*5.6*	*7.9*	*8.3*	*11.8*	*20.1*
36. *Melamphaes pumilus**	59	14	37	66	150	42	143	18	389	140	529
	27.8	*5.8*	*20.0*	*23.3*	*53.0*	*16.0*	*56.2*	*9.3*	*129.2*	*48.6*	*177.8*
37. *Melamphaes typhlops*	—	1	7	10	1	1	8	7	16	19	35
	—	*0.5*	*5.0*	*2.6*	*0.5*	*0.3*	*3.4*	*2.8*	*8.9*	*5.7*	*14.6*
38. *Melanostomiatid larvae*	—	—	—	—	5	1	1	—	6	1	7
	—	—	—	—	*1.8*	*0.3*	*0.3*	—	*2.1*	*0.3*	*2.4*
39. *Myctophum nitidulum*	26	—	31	—	26	2	85	—	168	2	170
	4.6	—	*8.2*	—	*16.0*	*0.3*	*8.2*	—	*32.4*	*0.3*	*32.7*
40. *Notolychnus valdiviae**	69	60	38	14	247	299	243	140	597	513	1110
	26.3	*51.3*	*27.9*	*5.0*	*127.0*	*105.6*	*52.4*	*68.5*	*207.3*	*179.1*	*386.4*
41. *Notoscopelus caudispinosus*	—	1	4	1	—	—	34	4	38	6	44
	—	*1.0*	*2.7*	*0.4*	—	—	*4.5*	*1.5*	*7.2*	*1.9*	*9.1*
42. *Notoscopelus resplendens*	7	12	9	7	—	1	—	—	16	20	36
	3.0	*7.7*	*6.0*	*2.6*	—	*0.3*	—	—	*6.0*	*2.9*	*8.9*
43. *Pollichthys mauli**	17	3	51	8	15	2	55	13	138	26	164
	8.3	*1.0*	*65.7*	*2.4*	*6.2*	*1.0*	*11.4*	*6.4*	*83.3*	*9.8*	*93.1*
44. *Poromitra capito*	1	4	3	4	4	4	53	20	61	32	93
	0.3	*2.0*	*1.3*	*1.7*	*1.3*	*1.3*	*17.1*	*7.8*	*19.7*	*10.8*	*30.5*
45. *Rhynchohyalus natalensis*	—	—	1	2	—	—	—	2	1	4	5
	—	—	*0.3*	*1.2*	—	—	—	*1.1*	*0.3*	*2.3*	*2.6*
46. *Scopeloberyx opisthopterus*	10	9	8	16	22	32	22	20	62	77	139
	5.5	*6.0*	*2.7*	*5.8*	*7.3*	*12.0*	*13.8*	*9.2*	*23.8*	*27.0*	*50.8*
47. *Sternoptyx diaphana**	17	21	24	84	116	87	53	66	210	258	468
	9.9	*9.3*	*13.9*	*26.9*	*45.7*	*32.4*	*19.0*	*24.5*	*78.6*	*83.8*	*162.4*
48. *Symbolophorus rufinus*	1	—	3	—	2	2	1	—	7	2	9
	0.2	—	*0.8*	—	*0.6*	*0.8*	*0.1*	—	*1.5*	*0.8*	*2.3*
49. *Taaningichthys bathyphilus*	—	2	—	2	2	3	—	2	2	9	11
	—	*2.0*	—	*0.7*	*0.7*	*1.3*	—	*0.9*	*0.7*	*2.9*	*3.6*
50. *Taaningichthys minimus*	2	1	1	5	2	3	3	2	8	11	19
	0.7	*0.5*	*0.4*	*1.4*	*0.6*	*1.0*	*0.9*	*0.8*	*1.9*	*3.2*	*5.1*
51. *Valenciennellus tripunctulatus*	—	—	—	—	10	6	19	—	29	6	35
	—	—	—	—	*3.7*	*3.1*	*6.8*	—	*10.5*	*3.1*	*13.6*
52. *Vinciguerria attenuata**	19	34	18	32	159	45	72	12	268	123	391
	11.7	*11.2*	*8.5*	*10.7*	*60.2*	*19.2*	*24.5*	*5.9*	*93.2*	*35.8*	*129.0*
53. *Vinciguerria poweriae**	16	—	42	5	33	7	22	2	113	14	127
	7.3	—	*28.0*	*1.5*	*11.2*	*2.3*	*5.5*	*1.0*	*44.7*	*4.8*	*49.5*
Total no. of individuals	725	643	784	807	2304	1743	2824	1152	6637	4345	10982
Total no./h	*348.5*	*304.4*	*507.0*	*268.2*	*960.9*	*640.5*	*672.6*	*499.5*	*2140.5*	*1408.2*	*3550.0*
Total hours of discrete-depth trawling	25.2	34.7	26.7	46.6	46.7	42.4	63.1	31.6	161.7	155.3	317
Mean no. of individuals captured per hour of discrete-depth trawling	28.8	18.5	29.4	17.3	49.3	41.1	44.8	36.5	41.1	28.0	34.6

14 with the IKMT and neuston nets. The 25 taxa contained in Table 3 each represent at least 0.5% of the total nonbladdered catch for at least one of the cruises 12, 13, or 14. This selected group comprises about 95% of the total IKMT/neuston nonbladdered catch in each of the three cruises. We recognize that, in addition to the three Cyclothone species which have fat-invested swimbladders as adults (Marshall 1960), certain of the nonbladdered taxa may ultimately be shown to possess a swimbladder.

Environmental Data

The center of the OA quadrangle at 32°N, 64°W lies 80 km (43 nautical miles (M)) east-southeast of Hamilton, Bermuda.

TABLE 3. Total catch of numerically predominant nonbladdered fish taxa in OA 12, 13, and 14 obtained with IKMT discrete-depth and oblique tows and neuston tows. Taxa included here each represent at least 0.5% of the nonbladdered taxa group catch with these nets in at least one of the experiments.

	Mesopelagic fish taxa	Spring, OA 14	Summer, OA 12	Winter, OA 13	Total
1.	Anguilloidei	0	137	0	137
2.	*Ariosoma sp.*	0	814	0	814
3.	*Chauliodus danae*	39	203	99	341
4.	*Chauliodus sloani*	126	357	87	570
5.	*Cyclothone braueri*	1522	4844	3352	9718
6.	*Cyclothone microdon*	579	976	712	2087
7.	*Cyclothone pallida*	315	486	190	991
8.	*Chauliodus pseudopallida*	55	130	52	237
9.	*Diplospinus multistriatus*	51	30	63	144
10.	*Evermanella indica*	0	59	3	62
11.	Flatfish larvae	1	406	2	409
12.	*Gonostoma elongatum*	12	35	29	76
13.	*Margrethia obtusirostra*	2	10	53	65
14.	*Melanostomias spilorhynchus*	0	188	0	188
15.	Muraenidae	0	61	0	61
16.	Myctophidae	41	10	42	93
17.	Myctophid larvae	298	502	226	1026
18.	*Nemichthys scolopaceus*	0	71	0	71
19.	*Nessorhampus ingolfianus*	2	56	0	58
20.	Paralepididae	1	187	28	216
21.	*Photostomias guernei*	17	13	3	33
22.	*Scopelarchus analis*	2	15	30	47
23.	*Scopelosaurus*	0	3	41	44
24.	*Serrivomer beanii*	43	134	91	268
25.	*Serrivomer brevidentatus*	19	33	12	64
	Total specimens T_1 (25 predominant nonbladdered taxa)	3125	9580	5155	17820
	Total specimens T_2 (nonbladdered taxa group)	3225	10421	5326	18972
	Percentage $(T_1/T_2) \times 100$	97	92	96	95

Water depths within the study area vary from about 2000 m in the northwest portion to 4500 m in the southeast. Representative vertical profiles of temperature, salinity, sigma-*t*, oxygen, and their depth derivatives have been constructed from data obtained by the Bermuda Biological Station (BBS) at a deep ocean hydrographic station located at 32°10′N, 64°30′W in the northwest quadrant of the OA quadrangle. A sample of these data obtained while OA 14 was in progress is shown in Fig. 1. Conditions below 400 m change little during the year. The seasonal near-surface variability in T, S, σ_t, and O_2 is illustrated in Fig. 2. Hydrographic conditions at this station are considered typical of broader open ocean areas of the northern Sargasso Sea. The oceanography of the sampling site and adjacent areas was reviewed by Brooks (1972) and Gibbs and Karnella (1987).

The diffuse light attenuation coefficient measured with a relative irradiance meter in near-surface waters in January 1971 was 0.0318/m (Stachnik 1971). Based on this figure, the nominal depth of the euphotic zone is 145 m, the depth at which the downwelling irradiance is reduced to 1% of the surface irradiance. Undoubtedly, this figure is subject to some seasonal variation.

Data Analysis

Raw size–depth data

To keep tape files and table printouts within bounds, the size cutoff limit for each species was set at 249 mm, an upper limit only rarely exceeded in catches with our nets. This size limit excluded from our total data set only 13 specimens belonging to seven different taxa. Depth coverage included the surface 0–1 m depth interval and from 11 to 20 irregularly spaced nominal 50-m depth intervals, different for each experiment. Lower limits of the deepest 50-m sampling interval ranged from 1100 to 1550 m, depending on the experiment and time of collection. An example of these data, which give nighttime size–depth information for the sternoptychid *Argyropelecus hemigymnus* in the upper portion of the sampling range, is given in Table 4.

Figures in the body of such tables (magnetic tape files) represent the catch per hour of 3-m IKMT fishing effort for fish of standard length l given in the left column. In our paper, IKMT catch per hour figures are divided by the conversion factor 3.62×10^4, the estimated volume of water (cubic metres) filtered per hour, to convert them to number of individuals per cubic metre at the nominal sampling depth. This conversion factor was calculated assuming that the towed net traveled 3 M in 1 h. Measured values 7.08 m^2 for the cross-sectional area of the IKMT mouth and 92% for filtering efficiency were used in computing this factor (Brooks et al. 1974). In estimating fish density in the 0–1 m depth interval from neuston catch per hour data, the same conversion constant was used, an arbitrary procedure not free of objection, but perhaps preferable to one based on refined assumptions about unknown fish distributions immediately below the surface.

Computer programs were written to calculate the size–depth distribution properties of individual species and arbitrary species groups during N/D measurement periods.

Normalized number densities and cumulative depth distributions

Let $n(z)$ denote the number density (or "abundance") of a particular species or species group, i.e. the average number of specimens per cubic metre found at depth z during either a nighttime or daytime period. Suppose the population is divided into nonoverlapping size classes corresponding to the various life stages of the species/species group. Let individuals in the sth life stage size class belong to the standard length range $l_1(s) < l \leq l_2(s)$ and denote their number density by $n_s(z)$. We then have

$$(1) \quad n(z) = \sum_s n_s(z).$$

The standing crop N of the species/species group between the surface and depth Z is defined as

$$(2) \quad N = \int_0^Z n(z)\, dz.$$

It represents the average number of fish in a vertical column of water of 1-m^2 cross-section extending from the surface to depth Z. The standing crop N_s for the sth life stage is defined similarly.

The standing crop values N and N_s vary from season to season changing the scales of the corresponding density profiles. To facilitate seasonal comparison of essential distribution features, it is convenient to deal with normalized profiles $\hat{n}(z) = n(z)/N$ and $\hat{n}_s(z) = n_s(z)/N_s$, which we term the "characteristic" density distributions of the species/species group and its sth life stage, respectively. Using these definitions and letting $\gamma_s = N_s/N$, the following expression for $\hat{n}(z)$ is obtained from Eq. (1):

$$(3) \quad \hat{n}(z) = \sum_s \gamma_s \hat{n}_s(z).$$

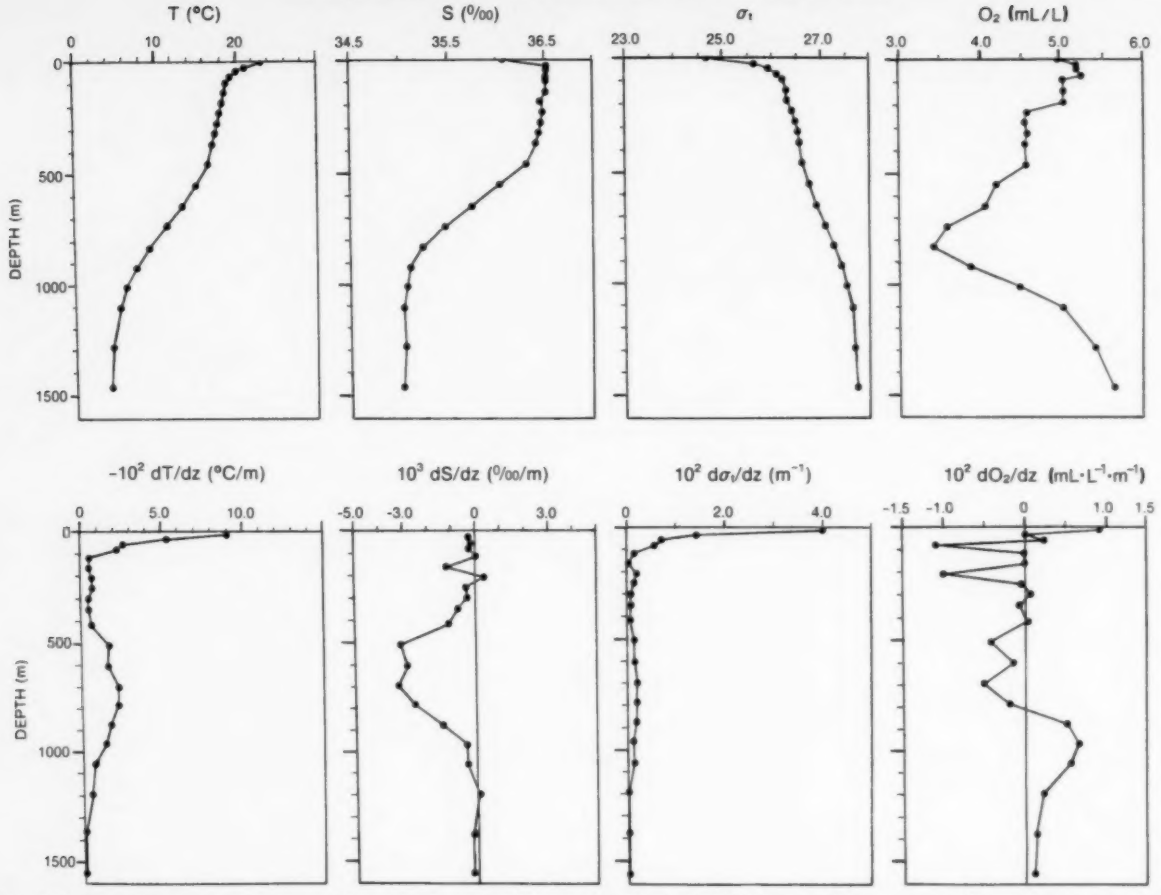

FIG. 1. Temperature, salinity, sigma-*t*, and oxygen data for OA 14 obtained by the BBS. Depth gradients computed from these data are in the lower portion of the figure.

The normalized, or characteristic, density functions $\hat{n}(z)$ and $\hat{n}_s(z)$ are analogous to probability density functions. The cumulative distribution of $\hat{n}(z)$,

$$(4) \quad C(z) = \int_0^z \hat{n}(z)\, dz,$$

represents the fraction of the standing crop N between the surface and depth z, with a similar interpretation for the cumulative density distribution $C_s(z)$ of $\hat{n}_s(z)$. The quartile depths z_{25}, z_{50}, and z_{75} for the characteristic distributions $\hat{n}(z)$ and $\hat{n}_s(z)$ are defined as the depths at which their respective cumulative distributions take the values 1/4, 1/2, and 3/4.

In evaluating integrals with discrete-depth data, sample number densities were assigned to the nominal representative depths 0, 25, 75, ..., 1525 m of their respective sample depth intervals in Table 1. For each daytime or nighttime experiment, density values are available for some particular set of irregularly spaced nominal depths $z_1 = 0, z_2, \ldots, z_k, \ldots, z_{tot}$. The standing crop was estimated using the following sum of trapezoid areas:

$$(5) \quad N = \frac{1}{2} \sum_{k=1}^{(k_{tot}-1)} [n(z_{k+1}) + n(z_k)]\Delta_k z$$

where

$$(6) \quad \Delta_k z = z_{k+1} - z_k.$$

The cumulative distribution function values $C(z_k)$ were estimated using a similar formula with appropriate changes in the summand and upper summation limit. Linear interpolation was used to estimate $C(z)$ at depths z between sample depths z_k and to estimate depths at which specified values of C occur. Similar formulae and calculation procedures were applied to sample density data for life stage size classes.

Depth preferenda for individual species

Let $n(z)$ be the number density distribution for a singe species. Suppose all nonzero values of $n(z)$ occur in the interval $z_{k1} \leq z \leq z_{k2}$. We define the preferendum depth $\bar{z}$ and the RMS deviation s_z from $\bar{z}$ by the equations

$$(7) \quad \bar{z} = \int_{z_{k1}}^{z_{k2}} z\, n(z) dz \Big/ \int_{z_{k1}}^{z_{k2}} n(z) dz$$

and

$$(8) \quad s_z^2 = \int_{z_{k1}}^{z_{k2}} (z - \bar{z})^2\, n(z) dz \Big/ \int_{z_{k1}}^{z_{k2}} n(z) dz.$$

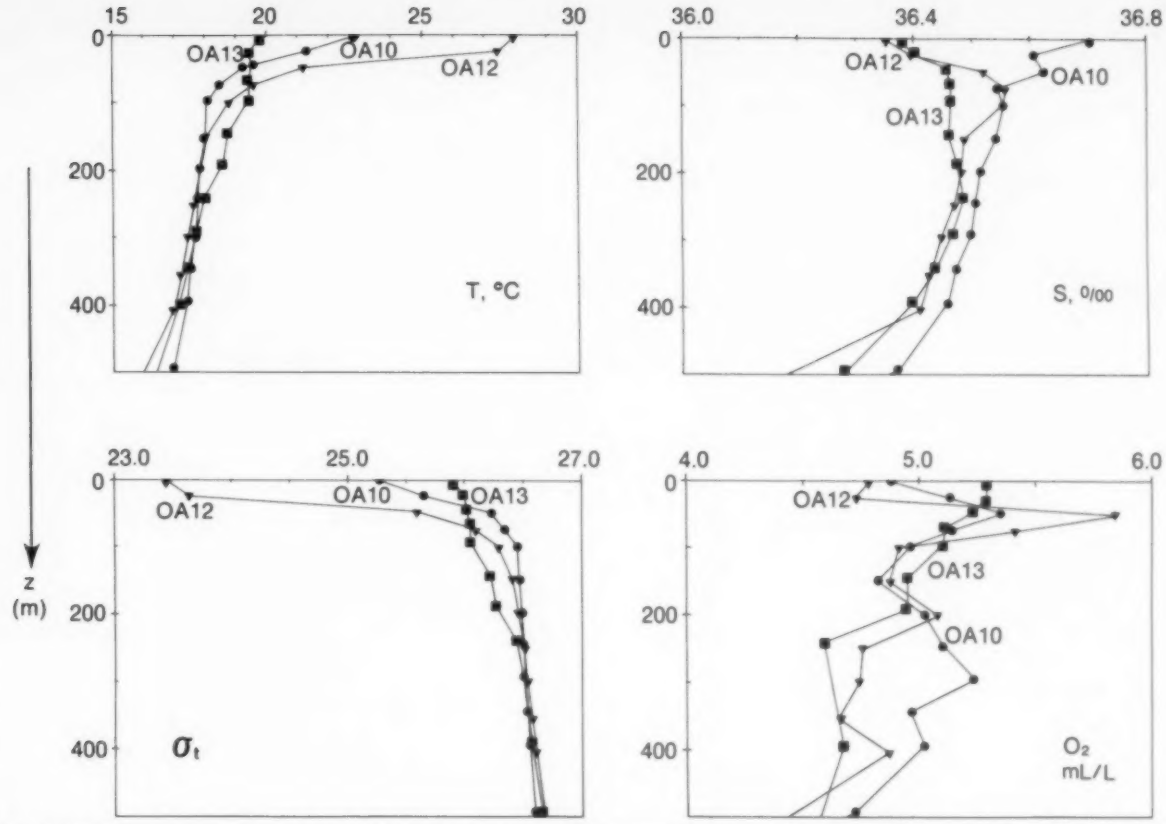

FIG. 2. Vertical distribution of T, S, σ_t, and O_2 from the surface to 500 m showing seasonal variability between spring (OA 10), summer (OA 12), and winter (OA 13). Data plotted are from BBS Nos. 325 (9 June 1970), 350 (30 August 1971), and 357 (28 February 1972), respectively.

Using Eq. (7), s_z is easily shown to be

$$(9) \quad s_z = [\overline{z^2} - (\bar{z})^2]^{1/2}$$

where

$$(10) \quad \overline{z^2} = \int_{z_{k1}}^{z_{k2}} z^2 n(z)dz \Big/ \int_{z_{k1}}^{z_{k2}} n(z)dz.$$

These integrals, like the ones above, were each approximated by a sum of appropriate trapezoid areas.

The determination of $\bar{z}$ and s_z was sometimes complicated by the character of the sample data. The size–depth table for an individual species was first inspected for "population clusters," i.e. concentrations of fish in more or less well-defined consecutive depth intervals. Most species have one, or perhaps two, clusters between the surface and the lowest sampling depths in the four experiments. In Table 4, a shallow cluster is evident. Inspection of tabular data for the 701–1450 m depth interval (not shown) reveals a second cluster between 951 and 1050 m. When many specimens are present in a cluster, and little is found at sample depths immediately above and below it, there is little difficulty in choosing depth limits for the preferendum calculation. However, when sample values were small and erratic, a number of factors were considered in subjectively deciding if a cluster were present, and if so, in choosing its depth limits. Briefly, these factors were (1) the shape of the number density and cumulative number density curves in the problematic depth region, (2) the fishing effort and number of specimens associated with each sample depth, (3) the length distribution (indicating the life stages of individuals in the depth region), (4) similarities/differences in clusters observed in other OA experiments at these depths, and (5) vertical distribution information for the species given by Keene (1970), Bond (1974), Howell (1975), and Karnella (1983). Estimates of $\bar{z}$ and s_z for clusters extending to the lowest sampling depths may be somewhat small because contributions from unknown portions of the clusters below these depths are not included in the calculations.

Occasionally one or perhaps a few specimens were captured at a single depth considerably removed from the main body of the size–depth distribution. In most cases, no depth preferendum value was assigned to these captures, since they could not reasonably be assumed to represent a separate population cluster and might, in fact, have been contaminants. It should be noted, however, that such captures often occurred at depths of about 1200–1500 m and may be the shallower individuals associated with a cluster below the maximum depth of discrete-depth sampling.

It is evident that depth preferendum determinations require subjective judgment to resolve ambiguities arising from sampling fluctuations and incomplete depth coverage. Nevertheless, as shown below, preferendum characteristics are useful for identifying migratory and nonmigratory species, for estimating changes in seasonal diel vertical migration ranges, and

TABLE 4. *Argyropelecus hemigymnus*, night. Number per hour of specimens of various standard length captured in discrete-depth samples from OA 13 (upper portion of profile only). Samples were taken from 1.5 h after sunset to 1.5 h before sunrise.

	Depth (m)														
Size (mm)	0 1	1 50	51 100	101 150	151 200	201 250	251 300	301 350	351 400	401 450	451 500	501 550	551 600	601 650	651 700
6	—	—	—	—	—	—	—	—	0.27	0.33	—	—	—	—	—
7	—	—	—	—	—	—	—	—	—	—	—	0.33	—	—	—
8	—	—	—	—	—	—	—	—	—	1.33	—	—	—	—	—
9	—	—	—	—	—	—	—	—	0.33	1.00	0.34	—	—	—	—
10	—	—	—	—	—	—	—	0.48	—	1.00	0.34	—	—	—	—
11	—	—	—	—	—	—	—	0.48	0.27	0.67	—	—	—	—	—
12	—	—	—	—	—	—	—	—	—	1.00	0.33	0.33	—	—	—
13	—	—	—	—	—	—	—	—	—	0.67	0.33	—	—	—	—
14	—	—	—	—	—	—	—	—	—	1.33	0.69	0.67	—	—	—
15	—	—	—	—	—	—	—	0.60	0.33	0.67	0.97	0.67	—	—	—
16	—	—	—	—	—	—	—	0.48	0.33	0.67	—	0.33	—	—	—
17	—	—	—	—	—	—	—	—	—	0.33	—	1.00	—	—	—
18	—	—	—	—	—	—	—	—	0.33	—	0.97	0.67	—	—	—
19	—	—	—	—	—	—	—	—	0.27	—	0.34	—	—	—	—
20	—	—	—	—	—	—	—	—	—	—	0.34	0.33	—	—	—
21	—	—	—	—	—	—	—	—	0.33	—	—	0.33	—	—	—
22	—	—	—	—	—	—	—	—	0.27	0.33	—	0.33	—	—	—
23	—	—	—	—	—	—	—	—	—	—	0.34	—	—	—	—
24	—	—	—	—	—	—	—	—	0.33	—	0.33	—	—	—	—
No./h	0	0	0	0	0	0	0	2.03	3.08	9.33	5.35	5.00	0	0	0
No. of hours	7.25	6.38	8.00	3.50	3.00	3.00	0	1.88	3.23	3.00	2.50	3.00	2.00	1.00	0
No. of specimens	0	0	0	0	0	0	0	4	10	28	14	15	0	0	0
No. of samples	42	7	9	2	3	3	0	2	3	3	3	3	2	1	0
Mean size	0	0	0	0	0	0	0	13.1	16.2	12.0	16.1	16.2	0	0	0

for specifying the location and mutual overlap of species depth niches.

Size distributions and statistics

Normalized standard length histograms for a species or species group caught at a single depth z_k, or in a depth range $z_{k1} \leq z_k \leq z_{k2}$, were computed from size–depth data such as shown in Table 4. The number per hour figures for a given standard length $l_i = i$ (1 mm) were summed for the relevant depth or depths to produce a weight factor for the ith class interval $l_i - 1/2 < l_i \leq l_i + 1/2$. This weight factor was normalized by dividing it by the sum of the weight factors for all l_i to produce $P(i)$, the probability that l lies in the ith class interval. Mean standard length $\bar{l}$ and root-mean-square deviations s_l from $\bar{l}$ were estimated in the usual way from the histogram amplitudes $P(i)$. Our histogram plots of $P(i)/\Delta l$ may be interpreted as probability density amplitude values averaged over successive Δl = 1-mm class intervals.

The skewness characteristic of many fish size distributions can often be substantially reduced by using the logarithmic size variable $x = \ln (l/1 \text{ mm})$ in place of l. Largely for this reason, transformation formulae were developed allowing optional plots of size histograms in log space with amplitudes representing average probability density values over successive class intervals Δx of chosen size. In log space, the ith class interval $\Delta_i x$ corresponding to the ith linear class interval $l_i - 1/2 < l_i \leq l_i + 1/2$ has the midpoint value $x_i = (1/2) \ln (i^2 - 1/4)$ and the same associated probability $P(i)$. The mean $\bar{x}$ and RMS deviation s_x were estimated from

$$(11) \quad \bar{x} = \sum_{\text{all } i} \left[\left(\frac{1}{2} \right) \ln \left(i^2 - \frac{1}{4} \right) \right] P(i)$$

and

$$(12) \quad \overline{s_x^2} = \sum_{\text{all } i} \left[\left(\frac{1}{2} \right) \ln \left(i^2 - \frac{1}{4} \right) - \bar{x} \right]^2 P(i).$$

Results

General Features of Midwater Fish Size–Depth Distributions

Combined bladdered and nonbladdered fish taxa groups

For purposes of illustration, we present results obtained in the spring cruise OA 14. At night, the combined bladdered and nonbladdered fish population is concentrated just below the surface with a peak at about 75 m in depth (Fig. 3A). Another, broader peak of lesser magnitude lies between about 575 and 775 m. During the day (Fig. 4A), population density peaks at a depth of about 575 m with a minor peak at about 775 m.

Except where number density $n(z)$ was extremely low, each depth interval sampled, whether day or night, usually contained individuals spanning a wide range of fish length (Fig. 3B and 4B). The distribution of fish lengths in nighttime samples (Fig. 3C) shows three more or less distinct peaks centered at about 10, 20, and 40 mm, respectively. The corresponding daytime distribution (Fig. 4C) is qualitatively similar, and standing crop values are nearly the same. Due to differences in N/D sampling capability, however, the population samples are not equivalent, as shown below.

Swimbladdered and nonswimbladdered fish taxa groups

The relatively high number of fish at 0 m nominal depth in the combined data at night (Fig. 3A) is due almost entirely to the presence of nonswimbladdered taxa (Fig. 3A^n). These taxa,

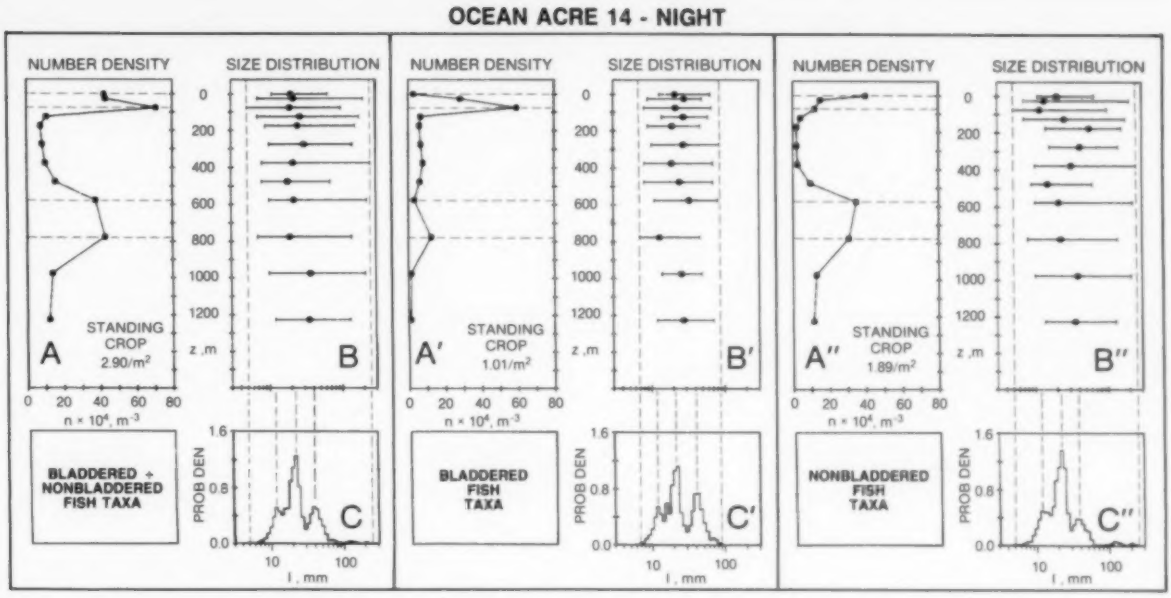

FIG. 3. OA Cruise 14, night. Comparison of number density – size distributions for the combined taxa, swimbladdered taxa, and nonswimbladdered taxa. Here, and in Fig. 4, size information and probability densities are expressed in terms of the logarithmic length variable $x = \ln(l/1\text{ mm})$. Means $\bar{x}$ (circles) and ranges (horizontal lines) are indicated for each sample depth.

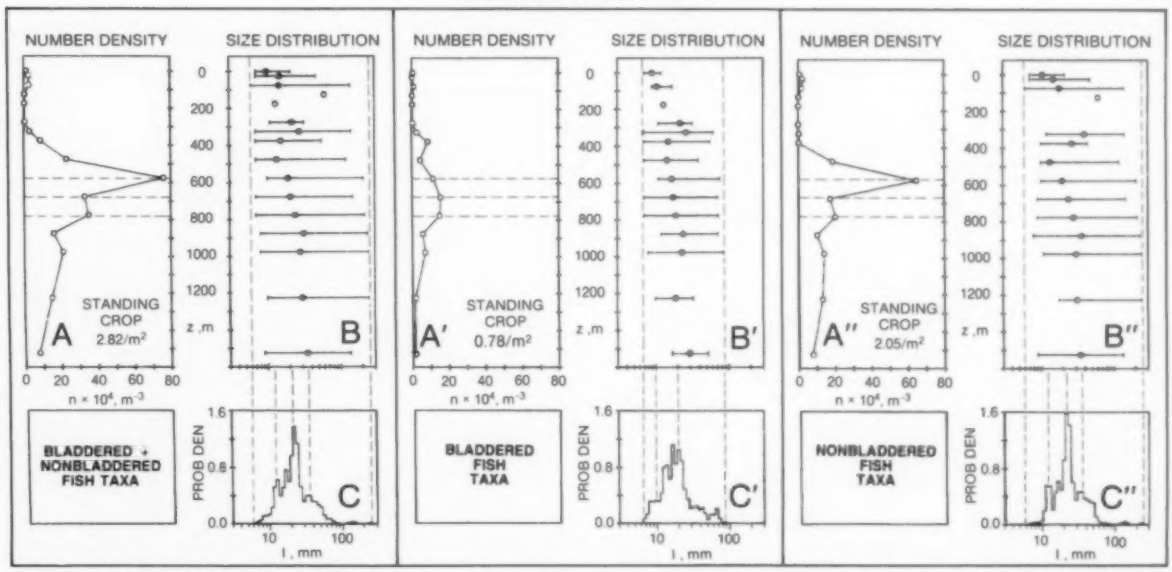

FIG. 4. OA Cruise 14, day. Comparison of number density – size distributions for the combined taxa, swimbladdered taxa, and nonswimbladdered taxa.

however, contribute little to the sharp peak observed at 75 m (Fig. 3A) where the bladdered taxa predominate (Fig. 3A′). The two groups appear to occupy relatively distinct subsurface depth niches at night. The broad peak between 575 and 775 m (Fig. 3A) is composed of a mixture of bladdered (Fig. 3A′) and bladderless (Fig. 3A″) fishes. Again, the nonbladdered fish show a preference for the shallower portion of the region of concentration. Standing crop values 1.89/m² (Fig. 3A″) versus 1.01/m² (Fig. 3A′) indicate a nearly 2:1 ratio in the numbers of nonbladdered and bladdered fish in the sampled water column. This high ratio is largely due to the inclusion of the three *Cyclothone* species in the nonbladdered group.

Rather surprisingly, peaks in the nighttime size distributions (Fig. 3C′ and 3C″) occur at approximately 10, 20, and 40 mm for both groups. In terms of the life stage size classes defined above for the swimbladdered group, the 10-, 20-, and 40-mm

TABLE 5. Daytime fish standard length intervals $\bar{l} \pm s_l$ (mm) near the top, middle, and bottom of the permanent thermocline for the bladdered plus nonbladdered, bladdered, and nonbladdered taxa groups (OA 14).

z (m)	T (°C)	Bladdered + nonbladdered	Bladdered	Nonbladdered
475	16.37	14.9 ± 10.1	16.3 ± 7.6	14.5 ± 10.6
775	10.54	28.9 ± 21.2	24.3 ± 17.7	32.2 ± 22.8
975	6.85	33.4 ± 27.8	26.6 ± 16.4	36.8 ± 31.4

peaks in Fig. 3C′ represent concentrations of larvae–postlarvae, juveniles, and adults, respectively. The relative magnitude of the larval–postlarval peak at 10 mm is very probably too low, as fish of the order of 10 mm or less in length tend to slip through the net. Throughout much of the water column, the size ranges of the swimbladdered taxa (Fig. 3B′) and the bladderless taxa (Fig. 3B″) tend to be fairly extensive, with the overall length range of the bladderless taxa being distinctly larger.

Corresponding plots for the daytime collections show that the pronounced peak at 575 m in the combined data (Fig. 4A) is due mostly to the peak in abundance of the nonbladdered taxa (Fig. 4A″), while the elevated levels of number density at 675 and 775 m result from an almost equal contribution from bladdered (Fig. 4A′) and nonbladdered individuals (Fig. 4A″). Although both groups are present between 575 and 775 m, there appears to be a definite preference of the nonbladdered fish for the shallower depth. Thus, during daytime hours as well, the two groups tend to remain separate to some extent. Nighttime and daytime peak displacement patterns in OA 10, 12, and 13 also usually suggest a tendency for the two groups to avoid concentration in exactly the same depth intervals.

During the day, a wide range of fish lengths is found at most sample depths within the 400–1000 m permanent thermocline region where the catch is appreciable (Fig. 4B′ and 4B″). The overall ranges for each group are similar to the corresponding ones at night (Fig. 3B′ and 3B″), with those for the bladderless group again being larger. There is a general tendency for mean fish size to increase with depth in both the bladdered and nonbladdered groups (Fig. 4B′ and 4B″; Table 5). Similar trends over the 400–1000 m depth zone occurred in OA 10, 12, and 13. At night this trend was not found in the bladdered group distributions whereas it was found in the nonbladdered group distributions for OA 10 and 13.

That the N/D sampled populations of the total midwater fish fauna are different is shown by the absence in the daytime (Fig. 4C′) of the adult component of the swimbladdered population represented by the 40-mm nighttime peak in Fig. 3C′. N/D populations of the nonbladdered fish group appear to be approximately the same, as suggested by the similarity of the corresponding size distributions and standing crops. Adult swimbladdered fish seem to be more capable of eluding the IKMT during daylight hours than nonbladdered fish of comparable size. The loss of adult swimbladdered fish in day catches also occurred in OA 10, 12, and 13 as shown by the relative reduction in the area of the daytime length distributions for $l \geq 40$ mm. An alternative explanation for this, viz. that adult swimbladdered fish migrate below the maximum sampling depths of 1000–1500 m, does not seem likely because the daytime depth preferendum zones $\bar{z} \pm s_z$ of the numerically dominant swimbladdered species shown below are usually well within these lower limits.

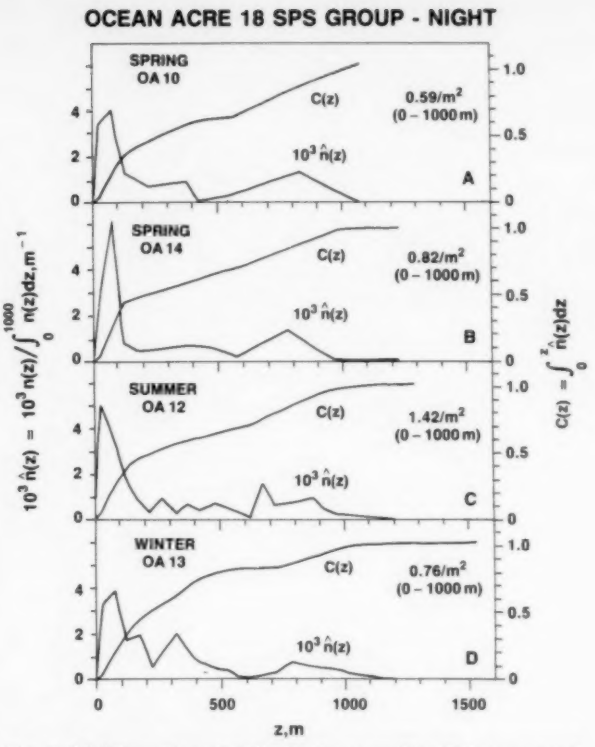

FIG. 5. Nighttime characteristic abundance profiles $\hat{n}(z)$, corresponding cumulative distribution curves $C(z)$, and standing crops between the surface and 1000 m for the 18 SPS group in spring, summer, and winter.

In what follows, we concentrate on the distribution properties of the bladdered group alone, which requires some comment. Subjective comparison of $n(z)$ for the two groups suggests that their N/D patterns tend to be characteristic. Nighttime $n(z)$ distributions for the bladdered group do not appear to be appreciably perturbed by marked seasonal variations in the nonbladdered group distributions. Also, the N/D bladdered group distributions do not appear to be particularly sensitive to seasonal variability in the standing crop ratio $(SC)_{NB}/(SC)_B$ which varies from 1.0 to 1.9 in the nighttime experiments and from 1.4 to 2.6 in the daytime ones. Biological interaction between the two groups is probably rather weak, so as a first approximation it seems reasonable to assume that their distribution properties are independent.

Seasonal Vertical Distribution Properties of Swimbladdered Fish

Size–depth plots such as those above for the 18 SPS in Table 2 are very similar to the corresponding plots for the 53 swimbladdered taxa. Distribution properties of the 53 taxa will usually be represented by those of the 18 SPS group in what follows.

Abundance distributions for the 18 SPS group

In Fig. 5 and 6, a common reference depth $Z = 1000$ m has been used in computing the indicated standing crop values N. Consequently, the areas under the normalized abundance profiles $\hat{n}(z) = n(z)/N$ from $z = 0$ to $z = 1000$ m are the same. Because some fish were caught below 1000 m, the cumulative

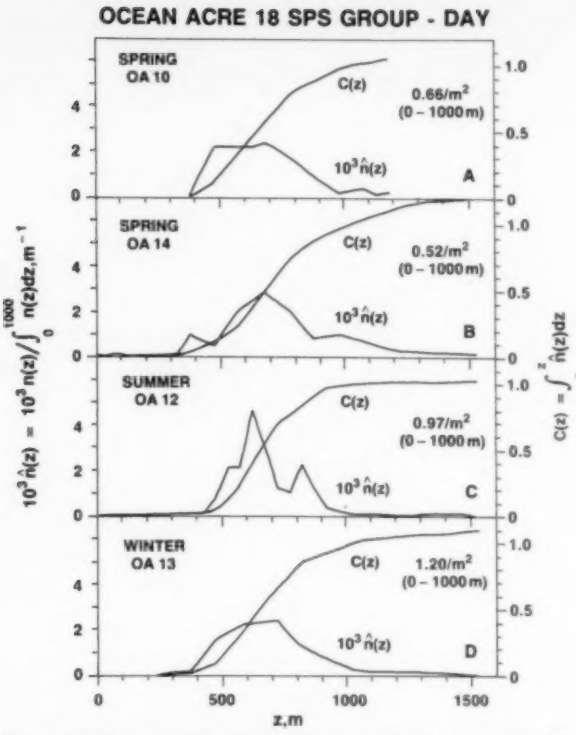

FIG. 6. Daytime characteristic abundance profiles $\hat{n}(z)$, corresponding cumulative distribution curves $C(z)$, and standing crops between the surface and 1000 m for the 18 SPS group in spring, summer, and winter.

distributions $C(z)$ somewhat exceeds the value $C(1000) = 1$ at depths below 1000 m.

The broad features of the N/D $\hat{n}(z)$ profiles are similar, despite seasonal variability in standing crop and oceanographic conditions (Fig. 2). The underlying similarity of these distributions is reinforced by the similarity of the N/D cumulative distribution curves $C(z)$ whose overall appearance may be expected to be less affected by random sampling errors than the $\hat{n}(z)$ curves. Qualitatively, these results suggest that between the surface and 1000 m, characteristic abundance distributions for swimbladdered fish taxa change little throughout the year at OA.

Year-round diel vertical migration properties of the 18 SPS group may be inferred from the $C(z)$ curves. During the day, 1–2% or less of the entire population lies between the surface and 300 m, while at night, over 50% of the entire population lies in this depth zone. Similar results are obtained for the 53 swimbladdered taxa.

Seasonal succession of size classes

In Fig. 7, the overall similarity in the distributions for the spring experiments OA 10 and 14, which are constructed from data collections separated by a period of 2 yr, suggests that the relative proportions of the various life stage size classes in a given season may change little from year to year. Adult fish clearly present in the spring are virtually absent in the summer OA 12 distribution. This indicates that adults spawn in the spring and subsequently die, producing a summer population composed mostly of larvae–postlarvae with a secondary peak of juveniles. Subsequent growth of individuals in these two life

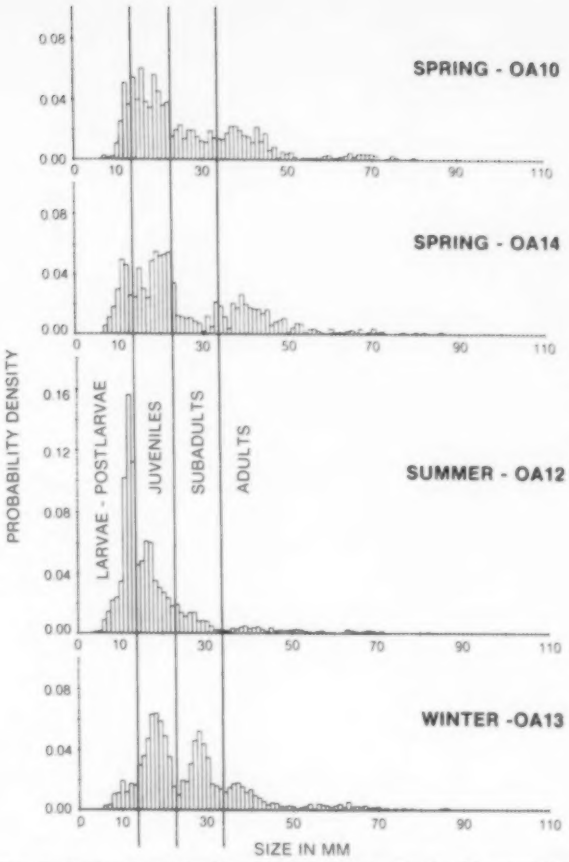

FIG. 7. Seasonal standard length distributions for the 53 swimbladdered taxa derived from all nighttime discrete-depth samples. Nominal size ranges for the life stage size classes are those derived for the 18 SPS group.

stages results in a preponderance of juveniles and subadults in winter (OA 13) accompanied by an increase in the relative proportion of adults due to the growth of subadults. Corresponding daytime size distributions for the bladdered taxa reveal these same general patterns except that adults are reduced in relative number, apparently due to their increased ability to avoid capture during daylight hours.

Abundance distributions of size classes

During nighttime periods, juveniles, subadults, and adults are concentrated between the surface and about 400 m depth in all seasons (e.g. Fig. 8C–8E). The dominant peaks in these $n_s(z)$ distributions usually lie within the nominal 0–150 m euphotic zone. Nighttime distributions of larvae–postlarvae are notably different (e.g. Fig. 8B). In all experiments they have a major peak in the 700–900 m depth interval and another prominent, but usually smaller, peak in the 0–100 m interval. A minor peak between 300 and 500 m is also always present. Only in the OA 12 summer experiment, where the standing crop of larvae–postlarvae is largest in both relative and absolute value, is the near-surface peak higher than its 700–900 m counterpart. During daytime periods, all four life stages are broadly and irregularly distributed for the most part over the 400–1000 m permanent thermocline region.

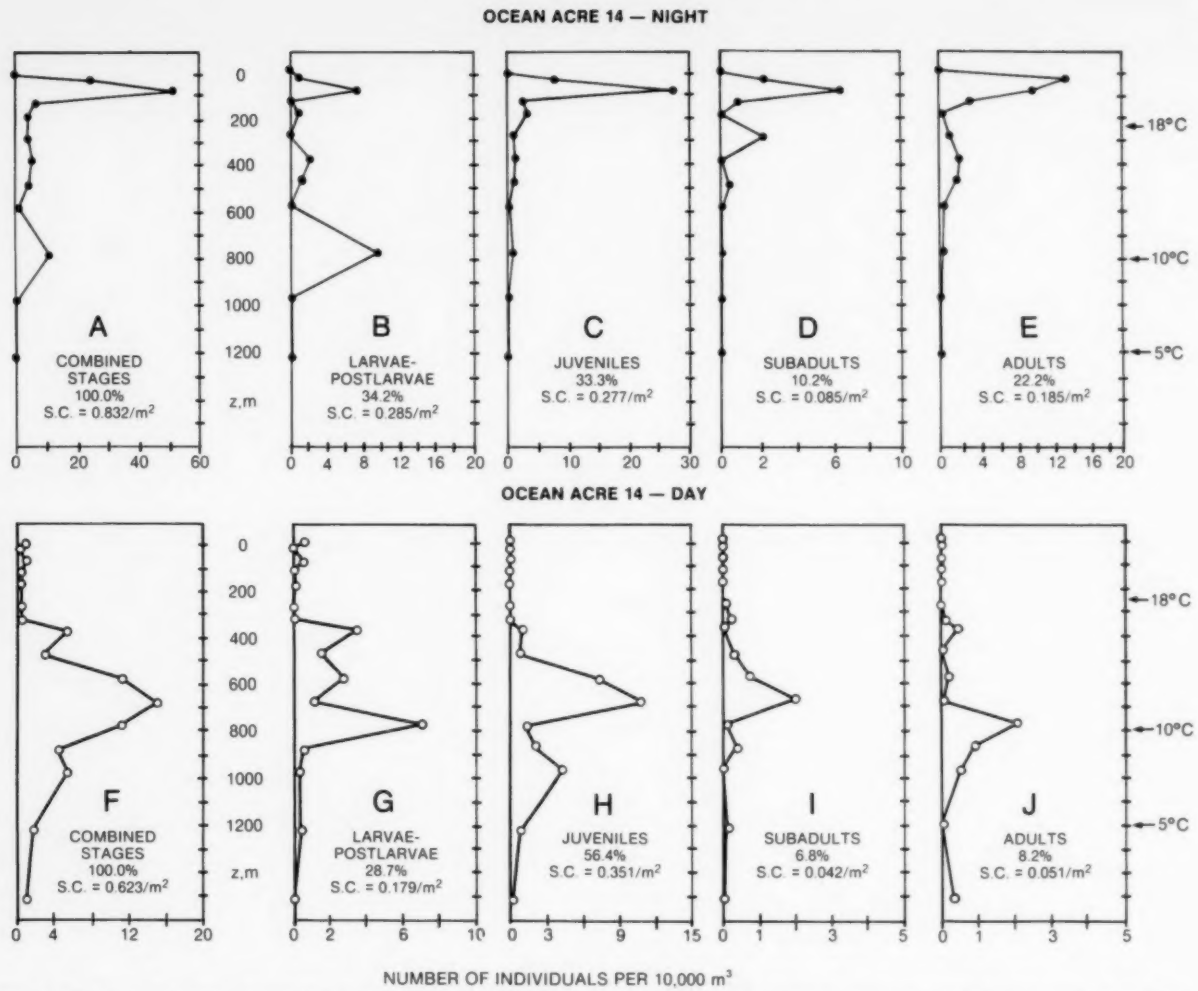

FIG. 8. OA Cruise 14. Abundance distributions for the 18 SPS group and its nominal life stage components, night (upper profiles) and day (lower profiles). Absolute and percentage values of standing crop (SC) are given for each profile. The depths of the 18, 10, and 5°C isotherms were 238, 799, and 1207 m, respectively, and the O_2 minimum occurred at 810 m.

Due to the small amount of data available for individual size classes, characteristic distributions $\hat{n}_s(z)$ are distorted by sampling fluctuations, so only a qualitative description of depth distribution and diel vertical migration properties is feasible for individual size classes. The following summary is based on data in Table 6 and percentage points read from cumulative distribution curves $C_s(z)$ not shown here.

During daytime periods, there is considerable overlap of the four life stage size classes in the 400–1000 m depth interval. Means $\bar{z}_{25} \leqslant z \leqslant \bar{z}_{75}$ of the central zones for the four experiments tend to lie successively deeper for the juvenile, subadult, and adult size classes, with the larval–postlarval zone falling in between. The fact that all life stage size classes have nighttime peaks in the 0–100 m depth interval and occasional peaks above 400 m as well indicates that diel vertical migration occurs in each size class throughout the year. Vertical migration is especially marked for the juvenile, subadult, and adult size classes of the population. Whereas more than 75% of each of these populations lies below 450 m during the day, more than 75% of each population lies above this depth at night year-round. (The nighttime adult distribution n_4 for the summer experiment OA 12 does not fit this pattern. Since the standing crop of adults (0.07/m²) is very small, this distribution is probably spurious and is discounted here.)

For the larval–postlarval size class, vertical migration is relatively weak during the spring (OA 10 and 14) and winter (OA 13), with over 75% of the population remaining below 400 m, both day and night. Only the upper portion of each daytime distribution appears to be involved in the upward migration, as suggested by the closeness of day/night values for the median depth z_{50} and for the 75% quartile depth z_{75}. In the summer (OA 12), when the larval–postlarval size class is the largest component of the population, migration is more pronounced. During the day, as in the other seasons, less than 25% of the population lies between the surface and 400 m whereas at night, 45% of the population is found in this depth interval. More of the upper portion of the daytime distribution now appears to be involved in the vertical migration because only day/night values of z_{75} remain essentially unchanged.

TABLE 6. Seasonal standing crops and 25, 50, and 75% quartile depths for individual and combined life stage size classes of the 18 SPS group.

	Night					Day				
	Postlarvae ≤13 mm	Juveniles 14–22 mm	Subadults 23–33 mm	Adults ≥34 mm	All life stages	Postlarvae ≤13 mm	Juveniles 14–22 mm	Subadults 23–33 mm	Adults ≥ 34 mm	All life stages
OA 10(spring)										
Standing crop (%)	31.3	39.6	11.3	17.8	0.6236/m^2	19.5	53.9	9.1	17.5	0.6964/m^2
Quartile depths (m)	641 (783) 928	65 (165) 368	58 (92) 126	85 (259) 433	87 (299) 733	682 (768) 877	492 (566) 644	631 (682) 738	743 (860) 991	538 (654) 775
OA 14(spring)										
Standing crop (%)	34.2	33.3	10.2	22.2	0.8320/m^2	28.7	56.4	6.8	8.2	0.6230/m^2
Quartile depths (m)	434 (684) 828	59 (102) 266	67 (122) 321	49 (100) 379	71 (223) 651	498 (697) 807	609 (716) 970	590 (667) 762	735 (829) 952	596 (717) 890
OA 12(summer)										
Standing crop (%)	49.7	35.1	10.5	4.7	1.463/m^2	37.0	39.9	19.1	4.0	1.006/m^2
Quartile depths (m)	96 (506) 747	65 (125) 363	64 (116) 322	334 (426) 669	80 (237) 680	554 (626) 750	577 (656) 762	628 (688) 795	796 (854) 915	582 (662) 784
OA 13(winter)										
Standing crop (%)	12.0	45.6	26.3	16.1	0.7869/m^2	17.1	40.8	32.7	9.5	1.337/m^2
Quartile depths (m)	465 (791) 900	104 (259) 415	45 (92) 170	169 (303) 421	89 (230) 443	608 (765) 889	509 (596) 702	609 (696) 793	750 (883) 1025	559 (676) 809
Mean (m)	409 (691) 851	73 (163) 353	59 (106) 235	159 (272) 476	82 (247) 627	586 (714) 831	547 (634) 770	615 (683) 772	756 (857) 971	569 (677) 815
RMS deviation (m)	197 (115) 70	18 (60) 54	8 (14) 88	110 (117) 114	7 (30) 110	68 (58) 56	48 (58) 123	16 (11) 24	24 (19) 41	22 (24) 45

Depth distributions of individual species

N/D depth distributions of each of the 53 numerically predominant swimbladdered taxa present in OA 14 are shown in Fig. 9 and 10. Only species with population clusters containing at least four specimens are represented. The number per hour abundance profiles for these species (Fig. 9B and 10B), apart from a proportionality factor, are essentially the same as the corresponding abundance profiles for all bladdered specimens (Fig. 3A′ and 4A′), showing that very few specimens were omitted.

At night, depth preferendum zones $\bar{z} \pm s_z$ form three distinct groups (Fig. 9A), one between the surface and about 100 m, another from about 200 to 500 m, and a third from about 750 to 1000 m. As may be seen from Fig. 5, nighttime abundance profiles $\hat{n}(z)$, not only in spring, but in summer and winter as well, contain three rather distinct peak regions more or less centered within these depth intervals. During the day, the species depth preferenda span the entire 400–1000 m permanent thermocline region (Fig. 10A), but correspondence with the peak structure in Fig. 10B is not so clear.

Seasonal N/D depth distributions for each of the 18 SPS are shown in Fig. 11. For each four-cruise set, daytime-specific preferendum depths $\bar{z}$ for 13 of the 18 species (viz. BSUB, BIND, LPUS, LDOF, NVAL, SDIA, LCUP, LGAU, VPOW, BPED, DATL, HBEN, and HHYG) differ by no more than 150 m, and for the first six species named, differences are less than 100 m. At night the situation is more complex. In one or more seasons, 12 species, mostly strong migrators, are seen to have a second deep-depth preferendum zone. Size intervals in both the shallow and deep zones often overlap nearly completely for many of these species (e.g. BIND, OA 12), indicating that vertical migration is not performed on a strict diel basis by fish of these sizes. For other species, the data suggest that the smaller size components of the population probably do not migrate on a regular diel basis, if at all (e.g. HHYG, OA 13). The shallow nighttime preferenda are usually located between the surface and 200 m, viz. for the species BSUB, BIND, CWAR, DATL, HBEN, HHYG, LPUS, LGAU, LDOF, PMAU, and VPOW. Except for HBEN, $\bar{z}$ for these species differs by less than 100 m in any four-cruise set. The deep nighttime preferenda, when they occur, usually lie between about 700 and 900 m (BIND, CWAR, DATL, HBEN, HHYG, LCUP, LPUS, LGAU, NVAL, SDIA, and MPUM). Where sufficient data exist for comparison, these preferenda too, for any four-cruise set, usually differ by less than 100 m.

Discussion

Properties of Size–Depth Density Distributions $n(l,z)$ Deducible from Discrete Depth Trawl Measurements

For a given faunal area, the size–depth properties of fish species groups (and of individual species as well) may be characterized theoretically by a two-dimensional density distribution $n(l,z)$ defined so that $n(l,z)dldz$ represents the average number of fish per unit volume with lengths $l \ldots l + dl$ in an indefinitely large horizontal water layer bounded by faces at depths $z - dz/2$ and $z + dz/2$. The density $n(l,z)$ may be pictured as a surface overlying an l,z plane. To facilitate comparison of N/D features of $n(l,z)$ in different ocean areas which are independent of standing crop N (whose values are often suspect), it is convenient to introduce a normalized density distribution $\hat{n}(l,z) = n(l,z)/N$ which is analogous to a bivariate

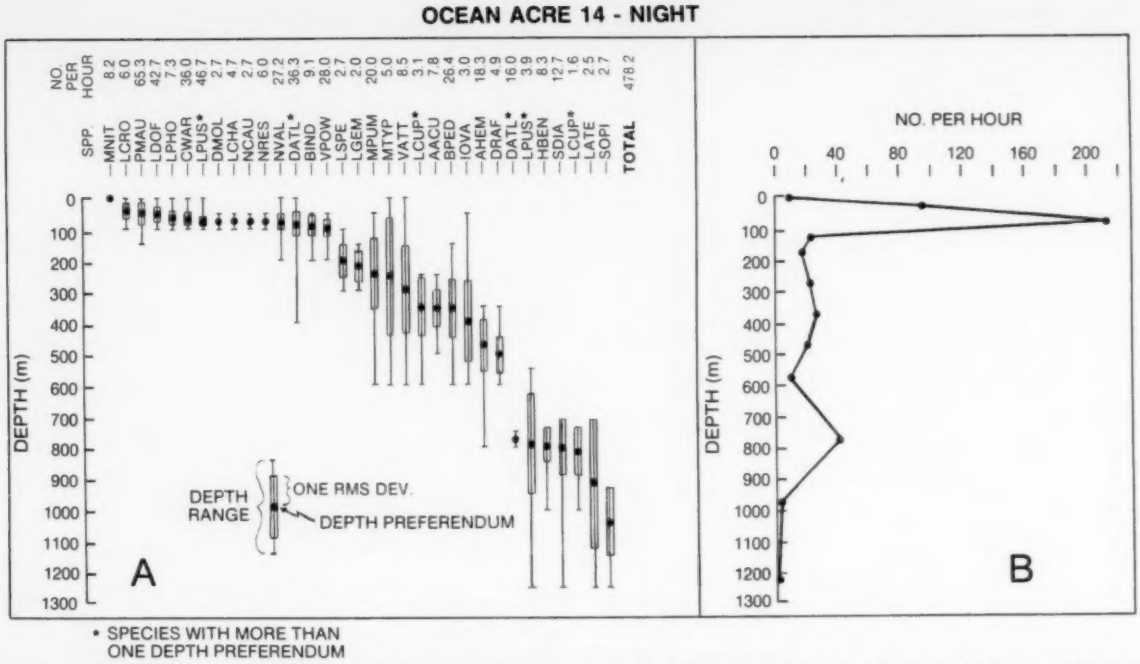

FIG. 9. OA Cruise 14, night. (A) Depth distribution properties of individual swimbladdered species in the 53 swimbladdered taxa group. For each species, the total number of specimens captured per hour at all sample depths within the indicated range is noted next to the species acronym (formed by combining the first letter of the genus name with the first three letters of the specific name in Table 2). Range limits denote the upper and lower end points, respectively, of the shallowest and deepest discrete-depth sample intervals for each population cluster. (B) Summed number per hour values for the taxa group at each sample depth.

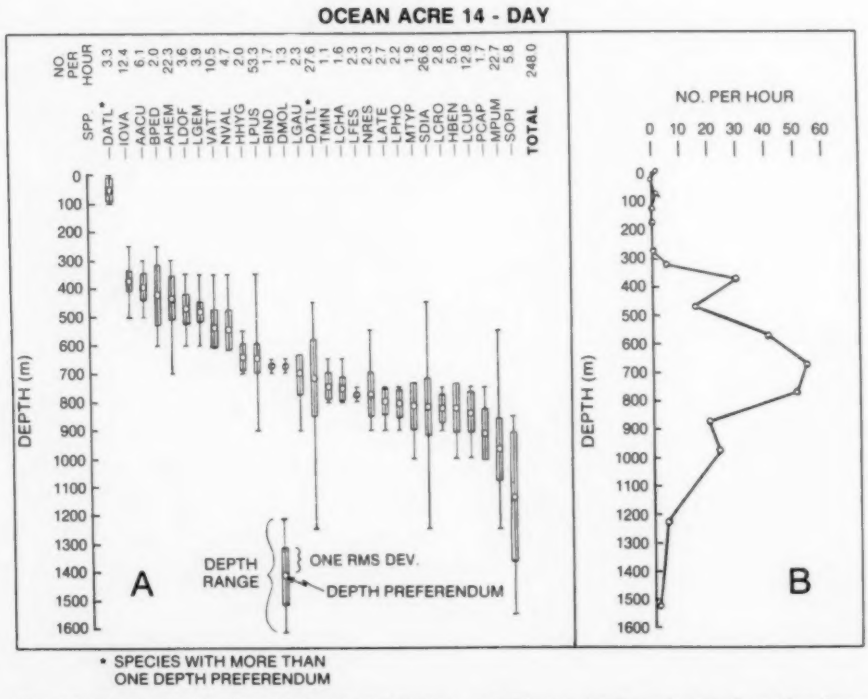

FIG. 10. OA Cruise 14, day. (A) Depth distributions and (B) associated number per hour abundance profile for the 53 swimbladdered taxa group. Acronyms here and elsewhere as in Fig. 9.

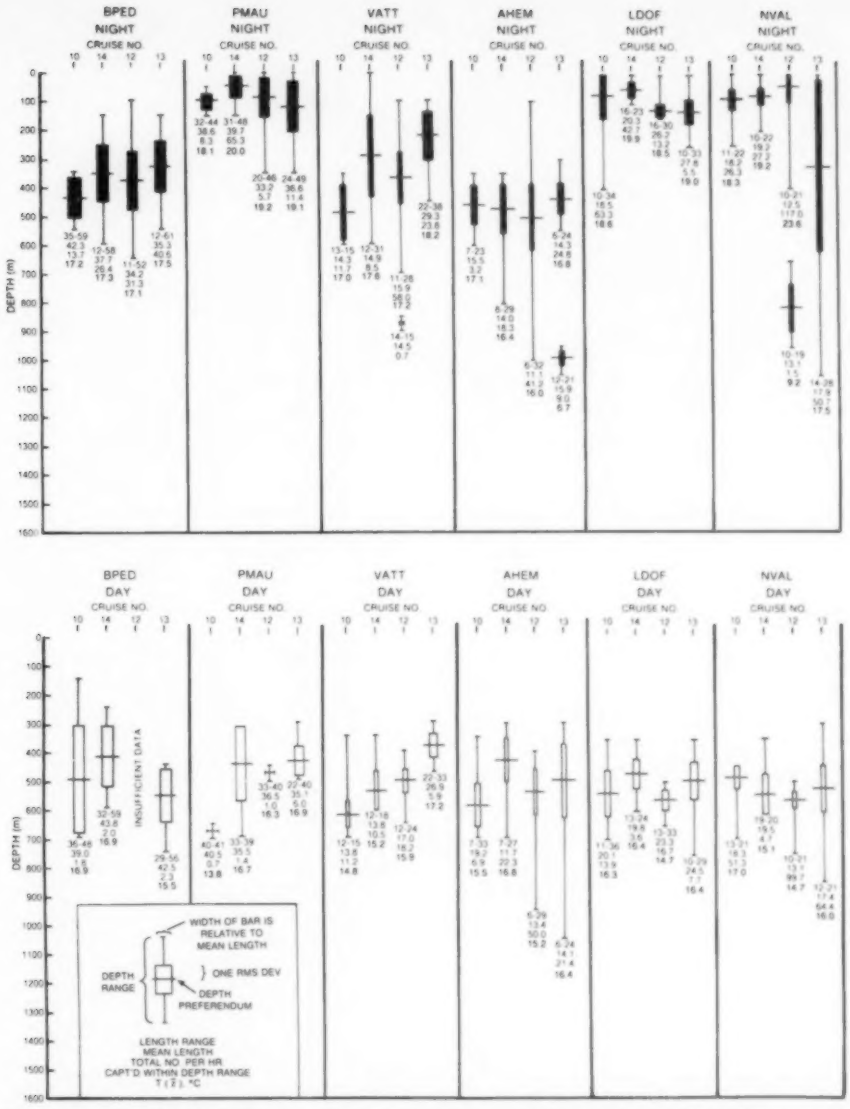

FIG. 11. Seasonal depth preferenda and associated measures of dispersion for the individual 18 SPS. The species are ordered according to increasing mean seasonal daytime depth preferendum values obtained in OA 10, 14 (spring), 12 (summer), and 13 (winter). Length ranges and mean lengths are in mm. (*Fig. 11 continued next page*)

probability density distribution in probability theory. Utilizing this analogy, one may formally write the distribution $\hat{n}(l,z)$ as the product of its z-marginal distribution $\hat{n}(z)$, obtained by integrating $\hat{n}(l,z)$ over all l, and the l-conditional distribution $p(l|z)$ for fixed z:

$$(13) \quad \hat{n}(l,z) = \hat{n}(z)p(l|z).$$

The factor $\hat{n}(z)$ is the characteristic abundance defined previously. Integrating $\hat{n}(l,z)$ over all z, one obtains the l-marginal distribution

$$(14) \quad p(l) = \int_0^\infty \hat{n}(z)p(l|z)dz.$$

The characteristic abundance distribution for the sth life stage size class is

$$(15) \quad \hat{n}_s(z) = \int_{l_1(s)}^{l_2(s)} \hat{n}(l,z)dl$$

where, as before, $l_1(s)$ and $l_2(s)$ denote the respective lower and upper length limits of the size class. In view of Eq. (13), $\hat{n}_s(z)$ is seen to be the fraction of $\hat{n}(z)$ represented by the area under the $p(l|z)$ distribution between $l_1(s)$ and $l_2(s)$.

Ideally, $\hat{n}(z)$, $p(l|z)$, and $\hat{n}_s(z)$ are obtained by perfect sampling of a narrow water layer of infinite extent at depth z. In practice, because only relatively small volumes of water can

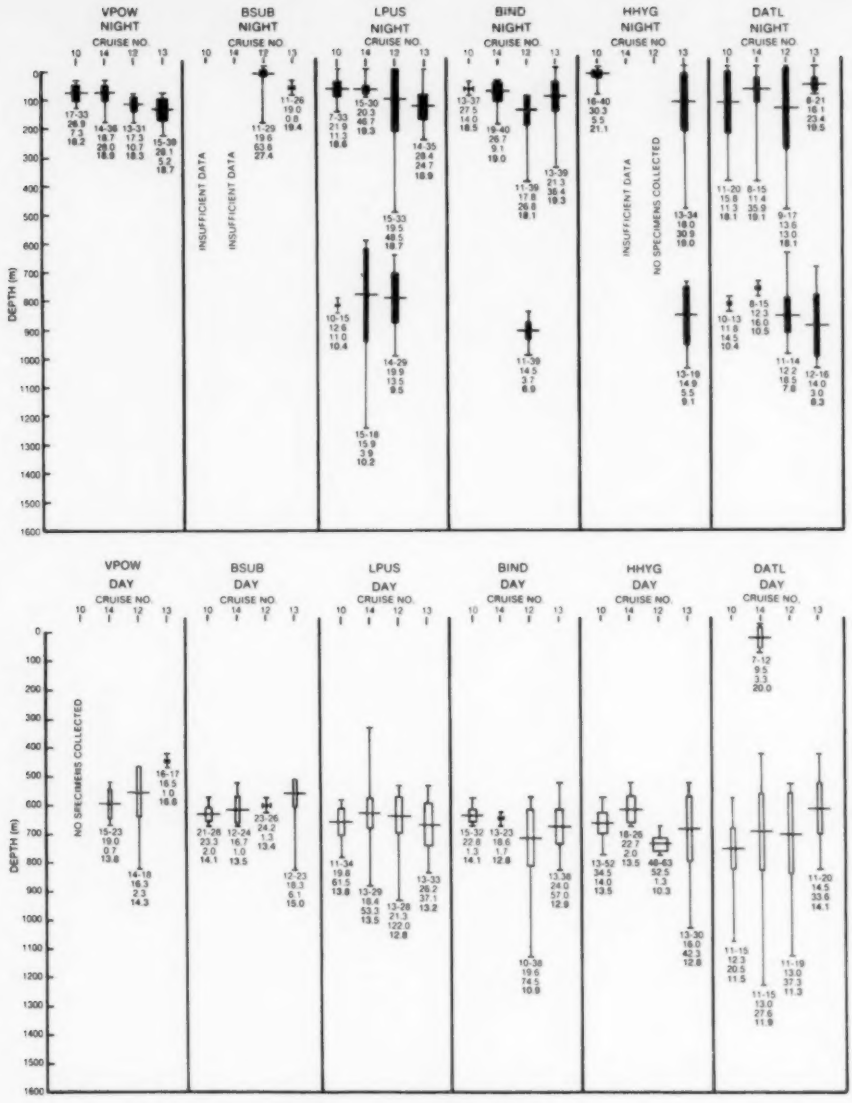

FIG. 11. (*Concluded next page*)

be sampled, large sampling fluctuations are present in measurements of these quantities. Consequently, not all properties of $\hat{n}(l,z)$ can be experimentally estimated with equal precision. The marginal distributions $\hat{n}(z)$ and $p(l)$, major features of $\hat{n}(l,z)$ which are estimated from the entire population of captured specimens, are likely to be defined relatively satisfactorily. However, $\hat{n}_s(z)$ and $p(l|z)$, which often are estimated from relatively few specimens, are not. Because individual species are usually poorly sampled in discrete-depth trawls, empirical characterization of $\hat{n}(l,z)$ is feasible, at most, only for species groups.

Seasonal Properties of $\hat{n}(l,z)$ for the Swimbladdered Species Group at OA in Relation to the Environment

Size–depth distributions $\hat{n}(l,z)$ for the 18 SPS group have two notable properties. The first is the marked N/D difference in characteristic abundance distributions $\hat{n}(z)$ and the seasonal consistency of these distributions. The second is the regular seasonal variation in the population size distribution $p(l)$ from which it may be deduced that there are also seasonal variations in $p(l|z)$.

Nighttime abundance profiles

The 18 SPS are planktivorous and are found mostly in the near-surface waters where zooplankton are concentrated. In spring, summer, and winter, $\hat{n}(z)$ has a prominent peak in the 150-m euphotic zone and a broad, relatively low-level peak between 400 and 1000 m. Except for the upper portion of the winter $\hat{n}(z)$ distribution (see below), there is little seasonal change in the basic shape of $\hat{n}(z)$ (Fig. 5).

Zooplankton biomass data of Menzel and Ryther (1961) taken near OA at midday in spring, summer, and winter are shown in Fig. 12A–12C. For purposes of relating fish and zooplankton concentrations in the water column, more complete zooplankton profile data are needed, but do not appear to be available.

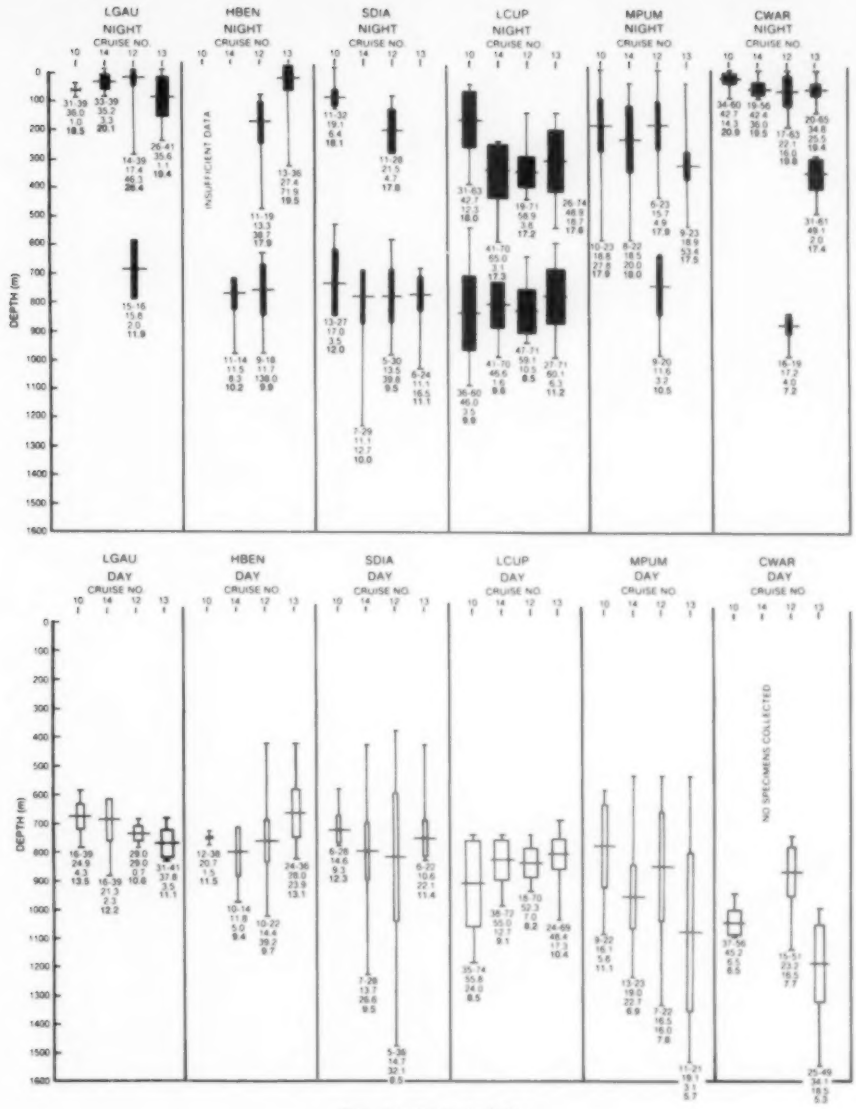

FIG. 11. (*Concluded*)

To repair this lack, we suppose that the N/D summer biomass profiles for copepods and other zooplankton groups in the eastern Gulf of Mexico obtained by Hopkins (1982) (Fig. 13 and 14) are fairly representative of at least spring and summer zooplankton distributions at OA. This assumption is qualitatively supported by the OA seasonal zooplankton studies of Deevey and Brooks (1971, 1977) covering the 0–2000 m water column in 500-m increments. Major zooplankton groups such as copepods, ostracods, and chaetognaths are prominent at both locations, with copepods predominating.

The diel vertical migration properties of zooplankton are clearly shown by the Gulf of Mexico data (Fig. 13 and 14). These data suggest that nighttime biomass profiles at OA would be much like the daytime ones in Fig. 12, except for a relative increase in biomass in the 0–150 m euphotic zone together with a small compensatory decrease at lower depths, say from 300 to 600 m. Based on this extrapolation, it may be argued that nighttime seasonal abundance profiles for the 18 SPS group in Fig. 5 are qualitatively similar to the corresponding nighttime seasonal distributions of zooplankton biomass. More particularly, from Fig. 5 and 13 the similarity of nighttime distributions $\hat{n}(z)$ and $\hat{b}(z)$ and of their respective cumulative distributions $C(z)$ and $B(z)$, particularly for the copepods, the largest component of the zooplankton, further suggests a causal connection between the nighttime distributions of fish and zooplankton.

Along these same lines, it seems likely that the anomalously broad winter profile $\hat{n}(z)$ (Fig. 5) is due, at least in part, to the broader distribution of subsurface zooplankton expected in winter. Near-surface water stability, as measured by $d\sigma_t/dz$, is strong in spring (Fig. 1) and summer, but is significantly reduced in winter by surface mixing, which may be inferred

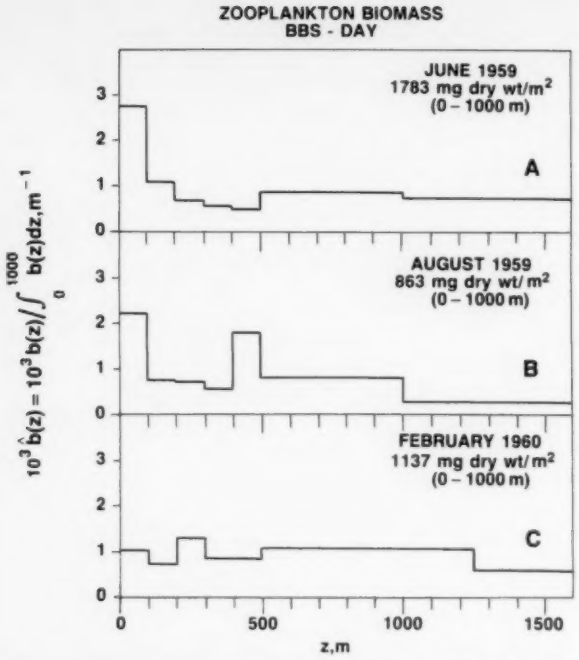

FIG. 12. Midday zooplankton biomass distributions from the BBS taken in spring, summer, and winter (constructed from Menzel and Ryther 1961, table 1). Normalized biomass densities $\hat{b}(z) = b(z)/SC$, where $b(z)$ is in mg dry wt/m^3 and SC is the biomass standing crop in mg dry wt/m^2 from the surface to 1000 m, are given for each season. Areas under each $\hat{b}(z)$ profile from the surface to 1000 m are equal.

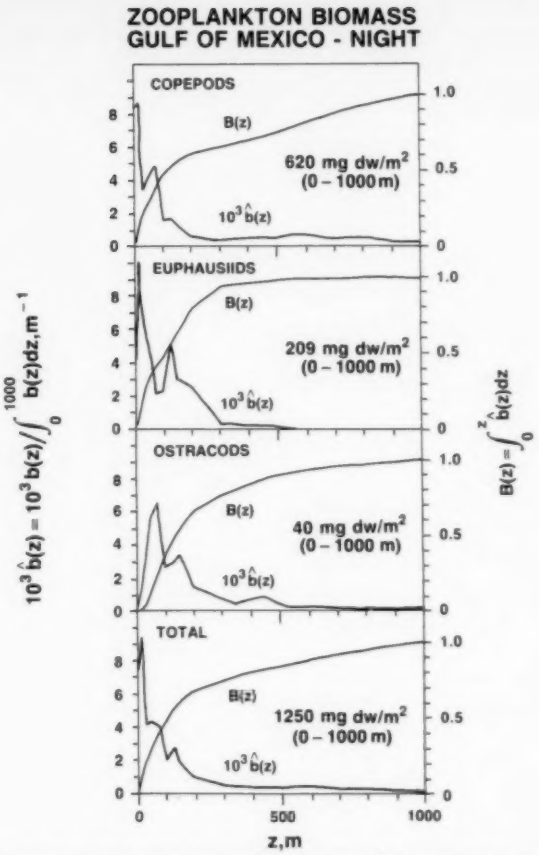

FIG. 13. Normalized nighttime biomass profiles $\hat{b}(z)$ defined as in Fig. 12 and cumulative distribution functions $B(z)$ for copepods, euphausiids, ostracods, and all zooplankton groups taken in the Gulf of Mexico during the summers of 1975–77 (constructed from Hopkins 1982, table 1). Standing crops from the surface to 1000 m are given for each group in mg dry wt/m^2.

from Fig. 2. Phytoplankton are down-mixed below the euphotic zone, and zooplankton grazing on this food source would be expected to attract nighttime fish predators over a more diffuse subsurface depth zone. Now, compared with the spring and summer distributions (Fig. 5A–5C), the form of $\hat{n}(z)$ and of $C(z)$ for winter (Fig. 5D) suggests an additional upward migration of a portion of the population from the lower part of the 250–750 m depth interval to the upper part of the interval, presumably in search of food. From an inspection of winter nighttime size class distributions, it appears that the migrators are largely juveniles and adults because their distributions are each bimodal, with a second subsurface peak around 300 m. Unfortunately, a nighttime winter zooplankton profile with the required depth resolution is not available to confirm these conjectures.

Daytime abundance profiles

In all seasons, daytime $\hat{n}(z)$ profiles have a broad peak ranging from about 400 to 1000 m (Fig. 6). The minimum in the summer profile between 700 and 800 m is probably not a permanent seasonal feature, but a sampling fluctuation, because sampling effort (3 h) was uniform at each sample depth between 525 and 1125 m and the same feature occurs in the $\hat{n}_s(z)$ distributions for the postlarval, juvenile, and subadult size classes which together make up 96% of the swimbladdered population.

During the day, much of the zooplankton biomass is concentrated between the surface and 400 m depth (Fig. 12 and 14), so the presence of the bulk of the bladdered fish populations in the 400–1000 m interval during daytime hours, which was commonly observed, must be due primarily to nontrophic factors, although some daytime feeding occurs (Hopkins and Baird 1977). Myctophid, sternoptychid, and other fish species observed from submersibles have been seen hovering nearly motionless during the day (e.g. Barham 1971). During daytime hours, many species apparently remain inactive in the relatively cold waters of the 400–1000 m dimly lit twilight zone to avoid attracting predators while at the same time conserving energy for growth and reproduction. The location and relative offset of depth preferendum zones of individual species during the day (Fig. 10 and 11) would appear to relate primarily to survival strategy. The observations of Badcock (1970) indicate that these patterns are the result of camouflage tactics determined, at least in part, by species skin color, reflectivity, and light-producing capabilities via photophores.

These considerations, together with repeated observations of diel vertical migration of mesopelagic fish in the world ocean, suggest that during the day, light intensity in the twilight zone is the principal environmental factor determining the daytime depth ranges of mesopelagic fish. Observations of sound-scattering layers support this view. For example, Dickson (1972) showed that the maximum daytime midlayer depths of two widespread 10-kHz scattering layers in the North Atlantic, one migratory and the other partially migratory, tended to be greater

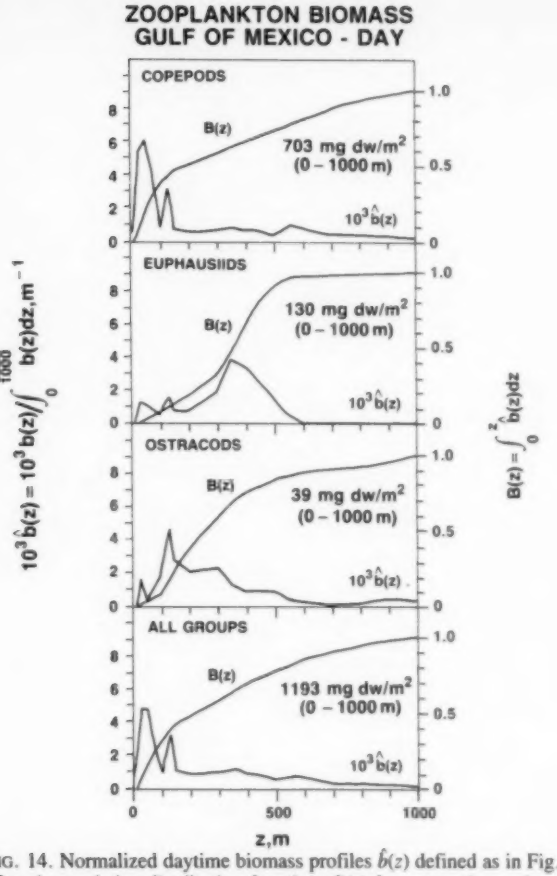

FIG. 14. Normalized daytime biomass profiles $\hat{b}(z)$ defined as in Fig. 12 and cumulative distribution functions $B(z)$ for copepods, euphausiids, ostracods, and all zooplankton groups taken in the Gulf of Mexico during the summers of 1975–77 (constructed from Hopkins 1982, table 1). Standing crops from the surface to 1000 m are given for each group in mg dry wt/m^2.

where water transparency, and hence light penetration, was greater.

The negligible values of $\hat{n}(z)$ below 1000 m at OA (Fig. 6) are probably mainly due to the fact that 1000 m is a representative depth for the threshold of the day/night visual perception of mesopelagic fish (Marshall 1971, 1979) and perhaps in some part to the fact that 1000 m is the approximate lower depth of North Atlantic Central Water at this location (Sverdrup et al. 1946).

Size distributions

Most of the individual species in the 18 SPS group have 1-yr life cycles, as determined from life history studies based on the OA collections (Bond 1974; Howell and Krueger 1987; Karnella 1987; Keene et al. 1987). During the year, these species have one or two spawning periods and some of them also spawn at low levels throughout much or all of the year. The spawning patterns are nonuniform, and as a result, all size classes of the species group are represented in some measure in each season. Such patterns reduce the competition for limited food resources among individual species (Gibbs et al. 1971a; Goodyear et al. 1972). More particularly, in a food-poor environment, partitioning of zooplankton food among fish at any depth can be expected to be enhanced, and hence favored by selection, if the range of fish size at that depth is matched to the size spectrum of zooplankton prey. The nighttime biomass distributions of the various zooplankton groups in Fig. 13, together with their size class distributions (Hopkins 1982, fig. 2), show that various kinds of food covering a wide range of size are available at each depth in the Gulf of Mexico (27°N, 86°W). Very likely, similar conditions hold at OA and many other deepwater locations. Thus, resource partitioning mechanisms in both time and space provide a qualitative explanation for the broadness of the seasonal size distributions in Fig. 7 (which crudely represent $p(l)$, Eq. (14)), as well as the wide range of size in seasonal $p(l|z)$ distributions found at many depths in the water column (e.g. Figs. 3B′ and 4B′).

While $p(l|z)$ is not experimentally well defined at many sample depths, it may be approximated in various ways using the relative weights $n_s(z)/n(z)$ of the different size classes present at depth z. For spring, these weights might be obtained from Fig. 8, for example. Because there are seasonal variations in size class standing crops N_s, and hence also $n_s(z)/n(z)$, seasonal variations in $p(l|z)$ as well as $p(l)$ must occur. Consequently, there are seasonal changes in the N/D size–depth distribution $n(l,z) = N\hat{n}(l,z)$ of the swimbladdered species group at OA, some of which are due to seasonal variations in the overall standing crop factor N. Changes in $n(l,z)$ are the underlying biological reason for seasonal variations in volume-scattering strength $S(z,f)$ and column strength $CS(f)$ observed at OA (Fisch and Dullea 1973; Fisch 1977) and elsewhere, e.g. at a deepwater location in the eastern Pacific Ocean (Vent 1972).

Quasistationarity of characteristic abundance distributions

In view of the nonstationarity of $n(l,z)$, it may seem paradoxical at first that the N/D characteristic abundance distributions $\hat{n}(z)$ for the 18 SPS group are approximately stationary year-round. From the definition of $\hat{n}(z)$ (Eq. (3)), it is seen that if N/D characteristic abundance distributions $\hat{n}_s(z)$ for each size class were identical, then regardless of seasonal variations in the relative standing crop factors γ_s, N/D profiles $\hat{n}(z)$ would remain the same throughout the year. From the general description of n_s profiles given above, excepting the deep portions of larval–postlarval profiles, nighttime n_s profiles are rather similar, as are daytime n_s profiles, making allowances for distortions due to sampling noise. This provides a qualitative explanation for the quasistationarity of N/D $\hat{n}(z)$ distributions, a point more convincingly made by the similarity of the N/D cumulative distribution curves $C(z)$ in Fig. 5 and 6, respectively. Anomalous features of the winter nighttime distributions $\hat{n}(z)$ and $C(z)$ discussed above are probably expressions of actual seasonal differences at OA.

Are similarities between $\hat{n}(z)$ *and hydrographic profiles necessarily physically significant?*

We have proposed that at night the form of $\hat{n}(z)$ is determined by the zooplankton distribution and that during the day it is determined by the underwater light field. Accepting these premises, similarities between $\hat{n}(z)$ and particular hydrographic variables at a given location do not necessarily signify causal connections, and hence may not be generally useful for prediction. Here we briefly note some striking, but physically misleading, similarities of this type found at OA that are likely to have analogs in other ocean areas.

At night, near-surface peaks in $\hat{n}(z)$ seen in the spring and summer profiles (Fig. 5) are similar to near-surface features of $-dT/dz$, $d\sigma_t/dz$, and, to some extent, also $O_2(z)$ (Fig. 1 and

2). However, in winter, a strong subsurface peak in $\hat{n}(z)$ is also observed, although the well-defined peaks in these environmental variables have been dissipated by near-surface mixing, as indicated by the T, σ_t, and O_2 profiles in Fig. 2. If winter data had not been taken, the physical roles of these hydrographic variables might have been misinterpreted.

Again, the 400–1000 m daytime $\hat{n}(z)$ distributions (Fig. 6), which are similar year-round to $-dT/dz$, $-dS/dz$, and $d\sigma_t/dz$ (e.g. Fig. 1), would appear to be significantly related to the permanent thermocline and the particular form of the oxygen minimum at OA. Yet, as shown below, similar daytime profiles occur at two Mediterranean sites where T, S, and O_2 are nearly constant between 400 and 1000 m. These characteristic hydrographic features at OA do not appear to determine the daytime form of $\hat{n}(z)$ in any direct sense, which supports Dickson's (1972) conclusion from a study of scattering layer and ocean transparency data that the overriding factor of importance for daytime distributions is light intensity, not local hydrographic conditions. Possibly hydrostatic pressure $P(z)$, the only environmental variable that is essentially the same at all locations, is also important.

Vertical Distribution Properties of Swimbladdered Fish in Other Ocean Areas

Depth distributions of individual swimbladdered species

Without detailed knowledge of specific spawning patterns and biological interactions, comparisons of specific depth distributions reported for various areas must necessarily be qualitative, especially in view of the differences in trawl equipment and measurement methodology usually involved. Consequently, we attempt to show only that the vertical distribution pattern of certain widespread bladdered species broadly conform to expectations based on the physical hypotheses discussed above. Since nighttime distributions of zooplankton and daytime measurements of underwater light are rarely made while trawl measurements are in progress, very simple environmental assumptions must be made.

Depth distribution data for the OA 18 SPS reported for a number of other open ocean locations between 12°N and 40°N will now be considered. In food-poor, midocean areas within this latitude range, where turbidity is low and insolation is fairly uniform, one may expect the euphotic zone to lie between the surface and about 150 m, as it does at OA. To first approximation, it seems reasonable to suppose that nighttime concentrations of zooplankton near the surface and daytime light levels in the 400–1000 m depth zone are much the same as at OA and consequently that specific N/D depth distributions of the 18 SPS at all such locations must be similar, if these factors are indeed the principal determinants of distribution properties. The hypothesis that other hydrographic factors such as T, S, etc., are less important, put forward, for example, by Dickson (1972) and suggested by results at OA, is automatically tested here to some extent because, as suggested by the temperature profiles in Fig. 15, hydrographic conditions in the various collection areas are very different from those at OA.

Depth distribution data for the 18 species in Fig. 16 include results from the Mediterranean (7 SPS, Goodyear et al. 1972; Nafpaktitis et al. 1977), off the Canary Islands (16 SPS, Badcock 1970; Badcock and Merrett 1976), off the Hawaiian Islands (5 SPS, Clarke 1973, 1974), and at Deepwater Dumpsite 106 (DWD-106) (18 SPS, Krueger et al. 1977). Also included are miscellaneous data labeled "other" which include

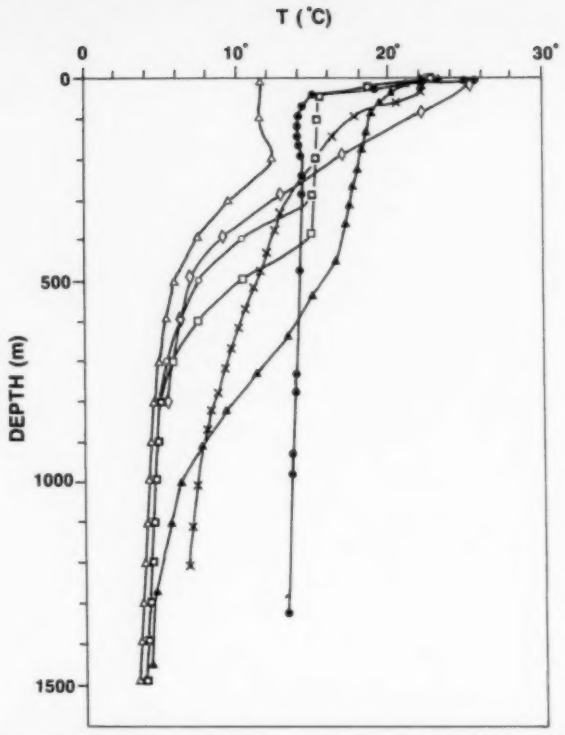

FIG. 15. Temperature profiles for some ocean sites where N/D vertical distributions of individual species and species groups (Fig. 16–18) are compared with those at OA: ●, Mediterranean (Tyrrhenian Sea site), September 1970 (Goodyear et al. 1972, p. 74); ×, Canary Islands, off Fuerteventura, November 1965 (Currie et al. 1969, table 2); ◇, west of Oahu, Hawaii (derived from Maynard et al. 1975, fig. 1); ▲, OA 14 (BBS No. 362, 7 June 1972). Profiles from the DWD-106 area: ○, western portion of a warm core eddy, July 1975; □, eastern portion of the eddy, July 1975 (derived from Goulet and Hausknecht 1977, fig. 16); Δ, slope water, February–March 1976 (adapted from Bisagni 1977, STD station 11).

results for the Gulf of Mexico (Hopkins and Baird 1985) and the Cariaco Trench (Pugh 1972). Depth plots for OA represent the overall maximum and minimum depth and preferendum zone ranges obtained from the seasonal plots in Fig. 11. Means of the seasonal depth preferenda are also given. For DWD-106, depth ranges represent the shallowest minimum and deepest maximum depths observed in two summer trawls (July 1975) and one winter trawl (February–March 1976). Depths of greatest abundance, when reported, are indicated by a rectangular bar.

It can be seen from Fig. 16 that the N/D distributions of the 18 species found at these various locations are generally similar to those found at OA, making allowances for differences due to various stages of ontological development. Despite the lack of measurement precision and detailed environmental information, the data in Fig. 16 seem to be consistent with the physical hypotheses stated above. DWD-106 data, however, are somewhat anomalous in that, for many of these species, upper limits of daytime deep preferendum zones, and sometimes even entire zones, lie at shallower depths than at OA. The dumpsite data were taken in the vicinity of 38°50′N, 72°15′W where water conditions are highly variable due to proximity to the Gulf Stream and where turbidity is higher than in the clear

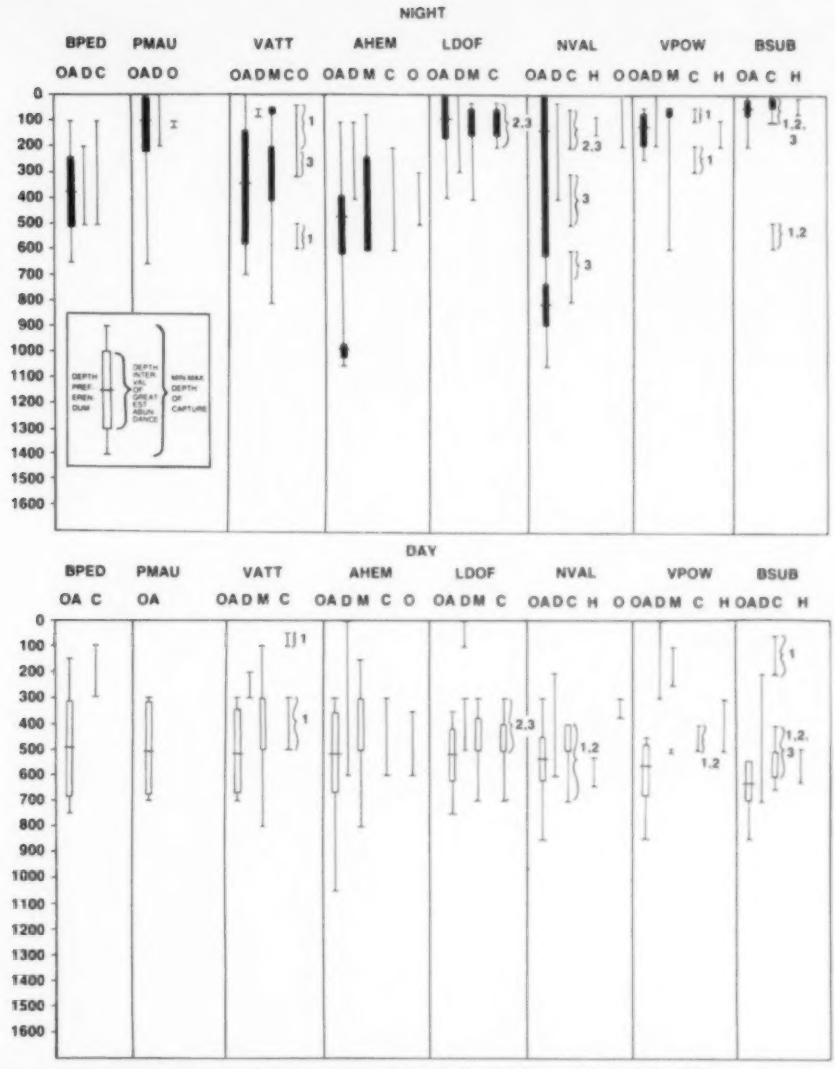

FIG. 16. Nighttime (upper) and daytime (lower) depth distributions of the OA 18 SPS at various ocean sites: OA, Ocean Acre; D, Deepwater Dumpsite 106; M, Mediterranean Sea stations; C, Canaries; H, Hawaii; O, other. Early developmental stages are indicated by 1, juveniles by 2, and subadults/adults by 3. See text for details and references. (*Fig. 16 concluded next page*)

waters of the North Sargasso Sea OA site. The tendency towards shallower daytime depths in less transparent water is expected on general physical grounds and is in accordance with the observations of Dickson (1972) and others. The effects of environmental differences at the DWD-106 location are more clearly demonstrated below where depth distributions of species groups are examined.

Abundance distributions of swimbladdered species groups

Data from the Balearic and Tyrrhenian seas and also from three different water masses in the vicinity of DWD-106 will now be compared with results from OA. Some general properties of the swimbladdered species groups are given in Table 7. Simpson's (1949) diversity index D provides a qualitative measure of the number of species that constitute most of the sampled population, in contrast with S_T, the total number of species found, many of which are present only in relatively small numbers. Here, $D = (\Sigma q_i^2)^{-1}$, where q_i is the sum of all number per hour catch rates at each sample depth for the ith species divided by the corresponding figure for all S_T species in the group. The dominant species with maximum q is indicated along with the "species dominance" value $d = q_{max}$ (Berger and Parker 1970). In these bladdered species groups the dominant species are myctophids except for the nighttime OA 14 and Tyrrhenian Sea groups in which the dominant species are gonostomatids.

Measurements in the Northeast Balearic and Tyrrhenian seas were made in late summer 1970 (Goodyear et al. 1972). From measurements at these and other sites in the Mediterranean, Kleckner and Gibbs (1972) identified a group of 23 swimbladdered species which includes the very numerous species *Cyclothone braueri* and *C. pygmae*. Since contributions to low-frequency scattering from *Cyclothone* are expected to be small due

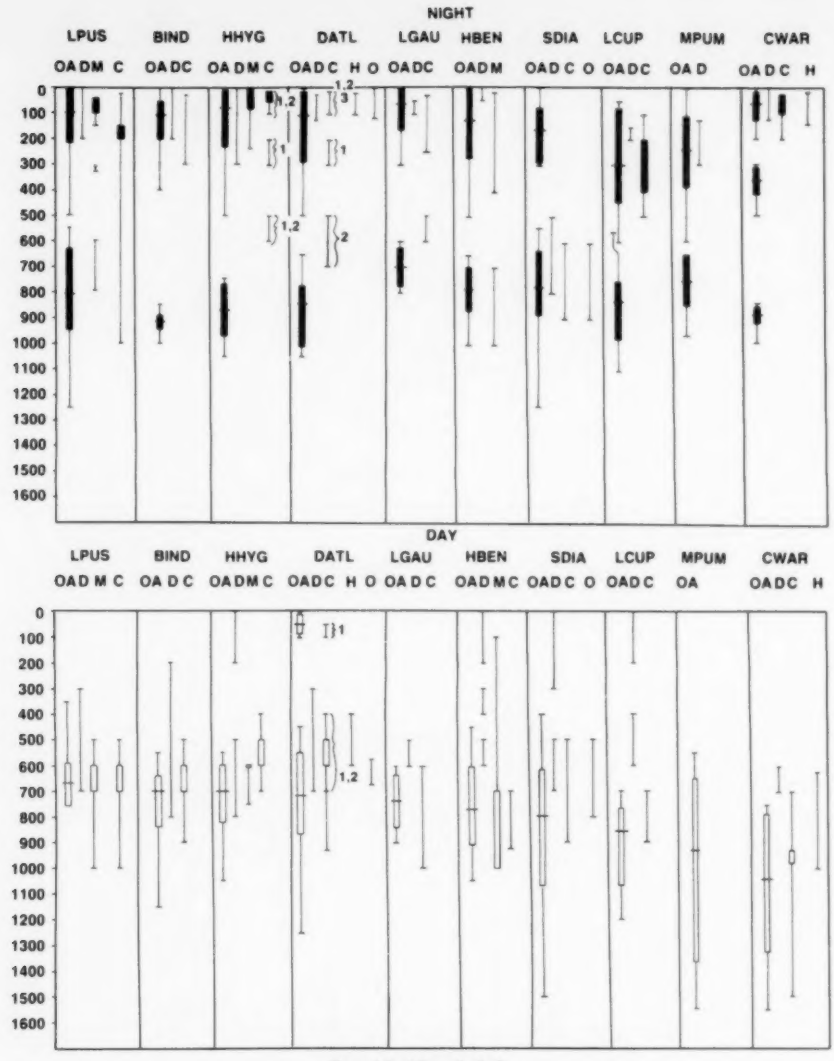
NIGHT
LPUS BIND HHYG DATL LGAU HBEN SDIA LCUP MPUM CWAR
OADM C OADC OADMC OADC H O OADC OADM OADC O OADC OAD OADC H
0 100 200 300 400 500 600 700 800 900 1000 1100 1200 1300 1400 1500 1600
DAY
LPUS BIND HHYG DATL LGAU HBEN SDIA LCUP MPUM CWAR
OADM C OADC OADMC OADC H O OADC OADMC OADC O OADC OA OADC H
0 100 200 300 400 500 600 700 800 900 1000 1100 1200 1300 1400 1500 1600

FIG. 16. (*Concluded*)

to fat investment of their swimbladders as adults (Marshall 1960), these species were excluded. The Balearic and Tyrrhenian groups consist of any of the remaining 21 species that happen to have been found. Group abundance profiles were constructed from tabulated abundance data for individual species found in Goodyear et al. (1972, appendices 2 and 3).

Nighttime abundance profiles for the Balearic and Tyrrhenian sites in Fig. 17 are very similar to the nighttime OA profiles in Fig. 5. The more complete Balearic profile clearly shows the three separate peak regions that appear to be associated with distinct concentrations of species subgroups at OA (Fig. 9). It is remarkable that the shape of characteristic abundance profiles at OA should be so closely reproduced at these Mediterranean sites despite differences in species composition, dominant species, diversity, and standing crop. Another notable biological difference is the much larger proportion of nonbladdered species present at the Balearic site ($SC_{NB}/SC_B = 5.4$) and at the Tyrrhenian site (5.6). Also, at the Balearic site the nonbladdered group is weakly migratory, with N/D peaks at 600 and 800 m, respectively, whereas at the Tyrrhenian site it is nonmigratory, with N/D peaks at 500 m. It would appear that bladdered group distributions are not appreciably influenced by the presence of relatively numerous nonbladdered competitors, as we have assumed.

Daytime bladdered group profiles from the Mediterranean (Fig. 18) are generally similar to those in Fig. 6 from OA in that most of the population lies between 400 and 1000 m. The lack of closer correspondence probably is mostly due to the low species diversity in the Mediterranean species groups: $D \approx 3$–4 as compared with $D \approx 7$–10 for the groups at OA. When D is low, prominent features of the group abundance profile are rather easily associated with the dominant species present. For example, in the Balearic profile, the large abundance value at 1000 m is mostly due to the dominant species *Hygophum benoiti* which at this depth has maximum abundance and constitutes 91% of $n(z)$. Again, the peak of 300 m is mostly due to *Vinciguerria attenuata*, the second-ranked species in the group making up 87% of $n(z)$.

TABLE 7. Parameters of swimbladdered species groups whose abundance profiles are plotted in Fig. 5, 6, 17, and 18. The number S_T of species present and, of these, the number S_{18} belonging to the 18 SPS group, Simpson's diversity index D, and the dominant species with its dominance value d (percentage) are given for each species group (Mediterranean data from Goodyear et al. (1972); DWD-106 data from Krueger et al. (1977), see text). Average towing time $\bar{T}$ (IKMT) for all subsurface discrete-depth IKMT samples in each set of measurements is also included.

	Nighttime				Daytime			
	S_T (S_{18})	D	Dominant species (d, %)	$\bar{T}$ (IKMT) (h)	S_T (S_{18})	D	Dominant species (d, %)	$\bar{T}$ (IKMT) (h)
North Sargasso Sea (32°N, 64°W)								
OA 10	18 (18)	9.4	LDOF (23)	1.90	17 (17)	6.9	LPUS (26)	2.42
OA 14	18 (18)	10.9	PMAU (16)	2.08	17 (17)	7.3	LPUS (26)	2.92
OA 12	17 (17)	9.7	HBEN (21)	2.50	18 (18)	7.4	LPUS (23)	2.28
OA 13	18 (18)	12.2	HBEN (15)	2.94	18 (18)	10.1	NVAL (17)	2.20
Northeast Balearic Sea (41°16′N, 06°57′E)	17 (5)	6.7	CMAD (25)	2.2	14 (5)	3.6	HBEN (44)	1.9
Tyrrhenian Sea (40°13′N, 12°28′E)	19 (7)	10.1	VATT (19)	2.5	17 (7)	3.7	CMAD (48)	3.2
DWD-106 (38°50′N, 72°15′W)								
Western eddy	20 (12)	4.9	LDOF (38)	0.51	15 (11)	8.6	LDOF (26)	0.57
Eastern eddy	27 (15)	12.9	LDOF (14)	0.34	23 (11)	12.1	LDOF (14)	0.46
Slope water	15 (7)	2.4	CMAD (64)	0.40	22 (13)	5.6	CMAD (39)	0.80

The similarity of Mediterranean and OA group abundance profiles is especially notable in view of the hydrographic as well as the biological differences involved. Temperature profiles at the Balearic site and at the Tyrrhenian site (Fig. 15) are very similar. After a rapid decrease from slightly different surface values, temperatures remain nearly constant from about 100 m to below 1000 m, very different from the permanent thermocline at OA. Salinity is also quite different, both Mediterranean profiles being offscale to the right relative to the OA 14 S-plot in Fig. 1, and showing little change below about 300 m. Dissolved oxygen at these sites peaks strongly in the euphotic zone, as it does in summer at OA (Fig. 2, OA 12), but it remains nearly constant in the 400–1000 m depth zone where the broad oxygen minimum region lies at OA.

Next we consider species group abundance data from the DWD-106 area 90 mi (145 km) east of Cape Henlopen, Delaware where underwater light levels and zooplankton distributions are expected to be qualitatively different from those at OA. The dumpsite lies over portions of the continental slope and continental rise, with depths ranging from about 1500 to 2700 m. Biologically and hydrographically, it is an area of transition between oceanic and coastal conditions. Hydrographic conditions are highly variable and unstable due to frequent aperiodic intrusions of Gulf Stream warm core eddies and meanders that may affect water properties to 800–1000 m. Biological data considered here were taken by Krueger et al. (1977) in the western and eastern portions of a warm core eddy present in the dumpsite area in July–August 1975. Data were also obtained in slope water present in February–March 1976. These data sets are respectively labeled WE, EE, and SW. Oblique, not horizontal, trawls were made within contiguous depth zones of variable width. Samples from wide depth zones judged unreliable for estimating $n(z)$ at nominal midzone depths are omitted in our abundance plots. Species group abundances, constructed from tabulations for individual species (Krueger et al. 1977, appendix 10), represent all captured bladdered species found in the list of 55 predominant swimbladdered taxa at OA (Brown and Brooks 1974). Detailed descriptions of the complex hydrography at the sampling sites were given by Goulet and Hausknecht (1977) and Bisagni (1977). Representative temperature profiles taken from these references are shown in Fig. 15.

While daytime downwelling irradiance at the water surface must be nearly the same in the dumpsite and OA areas because they are relatively close, the percentage decrease of downwelling irradiance with depth may be expected to be very different because of differences in optical water type. (The decrease for blue light (wavelength 465 nm) in waters of different optical type was illustrated by Jerlov (1976, fig. 71). Daytime downwelling irradiance levels, and hence also daytime fish concentrations, can thus be expected to lie at shallower depths in the more productive and turbid dumpsite waters. Some idea of probable differences in nighttime distributions of zooplankton biomass at the two locations can be obtained from the adult copepod abundance distribution measurements of Wishner and Allison (1986, fig. 4) taken in September 1982 in the northern edge, core, and southern edge of the Gulf Stream near 36°N, 73°W, east of Cape Hatteras. The shapes of these three N/D distributions are all generally similar to the N/D biomass distributions of Hopkins (1982) from the Gulf of Mexico (Fig. 13 and 14), but at night there is a very low level of copepod food available between 200 and 1000 m. Assuming similar conditions at the dumpsite location, one may expect a disproportionate amount of the nighttime population of feeding fish to be crowded into the near-surface region, compared with nighttime distributions at OA (Fig. 5).

N/D abundance distributions from the dumpsite area (Fig. 17 and 18) show diel differences analogous to those from OA and the Mediterranean, although species composition and hydrographic properties at the dumpsite are different. With regard to nighttime distributions, although sampling at lower depths was not complete, there appears to be a tendency for the winter SW and summer WE distributions as a whole to be more concentrated near the surface than the corresponding nighttime seasonal distributions at OA (Fig. 5). The seemingly contrary trend in the nighttime summer EE distribution may not be significant, since the average sampling time $\bar{T}$ = 0.34 h for this profile was quite small. The spiky appearance of these distributions is

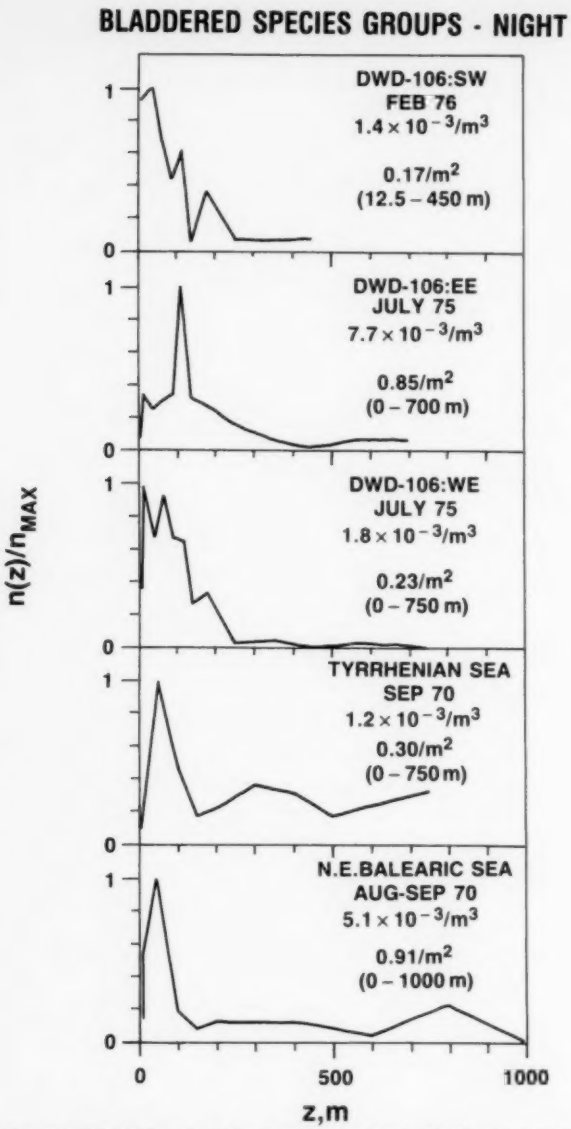

FIG. 17. Nighttime abundance profiles of swimbladdered species groups from the Mediterranean (Goodyear et al. 1972) and DWD-106 (Krueger et al. 1977). All these data were obtained with 1-m neuston and 3 m IKMT nets similar to those used at OA. Standing crops estimated from each profile and peak values used for normalization are indicated. See text and Table 7.

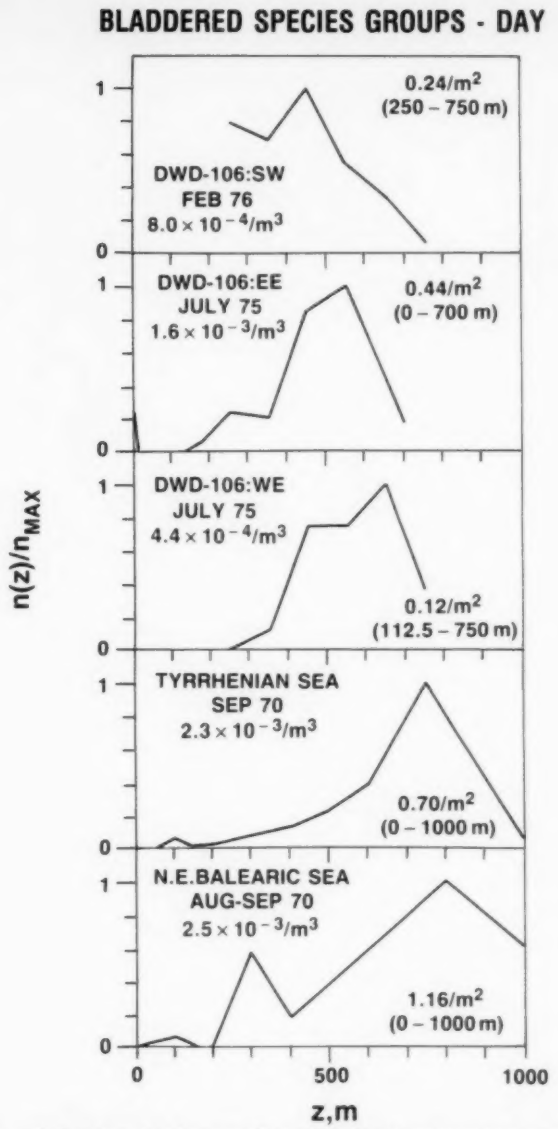

FIG. 18. Daytime abundance profiles of swimbladdered species groups from the Mediterranean (Goodyear et al. 1972) and DWD-106 (Krueger et al. 1977). All these data were obtained with 1-m neuston and 3-m IKMT nets similar to those used at OA. Standing crops estimated from each profile and peak values used for normalization are indicated. See text and Table 7.

probably caused partly by small sample fluctuations (note the small standing crop values and small average sampling times at each sample depth) and partly by low species diversity (Fig. 17; Table 7). In particular, sampling fluctuations due to patchiness very probably acount for the prominent spike in the EE data at 112.5 m where the tow duration was only 8 min. Towing times for sample depths immediately above and below this depth were 12 and 7 min, respectively, and abundance values at these depths are seen to be much lower and nearly equal. Daytime abundance distributions at the dumpsite (Fig. 18) all appear to be concentrated at shallower depths than daytime distributions at OA (Fig. 6) as expected. Again this judgment is somewhat subjective because depth coverage at the dumpsite is incomplete.

The abundance distributions of the bladdered and nonbladdered species groups seem to be relatively independent, as at the OA and the Mediterranean sites. Standing crop ratios SC_{NB}/SC_B for the N/D profiles ranged from a minimum of 2.5 to a maximum of 8.6.

Biological and Bioacoustic Implications

At OA, the distinctive N/D abundance distributions of the swimbladdered species group result from diel vertical migration

patterns of its constituent species. These patterns appear to be determined chiefly by the location of readily available zooplankton food at night and the need to keep to deeper, dimly lit waters during the day, largely to avoid predators. In widely separated locations, where nighttime distributions of zooplankton and daytime levels of underwater light are believed to be similar, available measurements for the OA 18 SPS suggest that the N/D depth distribution patterns of these species remain much the same, although the depth profiles of temperature, salinity, and dissolved oxygen may be very different.

Of particular physical interest is the possibility, suggested by our limited data for bladdered species groups, that N/D size–depth distributions $n(l,z) = N\hat{n}(z)p(l|z)$ may have certain similar features in different ocean areas, independent of the particular species in the group, so long as $D \geq 7$, say. At OA, resource partitioning in time and space seems to be the underlying ecological imperative responsible for the structure of $n(l,z)$. Individual species have noncoincident overlapping seasonal depth niches both day and night, thereby reducing competition. Minor seasonal variations in the overall organization of these depth niches throughout the year, despite seasonal changes in the occupants of the niches, their standing crops, and also hydrographic conditions, appear to be the reason for the quasistationarity of $\hat{n}(z)$ at OA. The presence of all fish size classes in the water column throughout the year, reflected in the broad l-limits of $p(l|z)$, is another manifestation of resource partitioning. Due to area-dependent patterns of primary and secondary production, surface mixing, and fish spawning cycles, $n(l,z)$ will generally be nonstationary in time with more or less pronounced seasonal variability in N, $p(l|z)$, and $\hat{n}(z)$. However, in food-poor, midocean areas with many species, the need for bladdered species groups to partition resources in order to remain viable must largely determine the form of $n(l,z)$, as at OA. Thus, in such areas, the general features of $\hat{n}(l,z)$ are probably like those at OA, as suggested by the similarity of Mediterranean and OA characteristic abundance profiles $\hat{n}(z)$ for different bladdered groups. However, in more productive, turbid areas near coasts where upwelling occurs, or in unstable areas where strong currents and turbulence are present, as at DWD-106, nighttime zooplankton distributions and daytime underwater light levels may be very different from those at OA. Changes in the N/D forms of $\hat{n}(z)$ in accordance with these differences must be expected, and the form of $p(l|z)$, about which we can say little, may now be determined by different ecological factors. However, data from the three different water masses near the dumpsite suggest that diel vertical migration of bladdered species groups will still occur and, as a result, that N/D forms of $\hat{n}(z)$ will at least crudely resemble those at OA.

Bioacoustic implications of these results and conjectures follow directly from the form of the volume-backscatter coefficient $s_v(z,f)$ which can be expressed as

$$(16) \quad s_v(z,f) = N\,\hat{n}(z)\,\tau(z,f)/d^2$$

where s_v is in (metres)$^{-3}$ and unit dimensional length $d = 1$ m. The quantity $\tau(z,f)$ in (metres)^2 is the average target strength of swimbladdered fish (or, more precisely, their gas-filled swimbladders) at depth z. It depends on $p(l|z)$, the swimbladder size allometry properties of the bladdered species group, and the acoustic cross sections of swimbladders of various size at depth z (see Saenger 1988 for details). Column strength CS(f), the vertical integral of $s_v(z,f)$ from the surface to the lowest depth where $\hat{n}(z)$ is appreciable, has been sampled throughout the world ocean (e.g. Chapman et al. 1974). In midocean regions between 40°S and 40°N, where mesopelagic species abound, the diel frequency spectra of CS(f) tend to have distinct, relatively uniform features within the boundaries of each faunal province (Backus and Craddock 1977) characterized by some particular homogeneous group of bladdered fish species. Observed diel and seasonal variability in CS(f) occurs due to the different N/D forms of $\hat{n}(z)$ and seasonal variations of N, $p(l|z)$, and possibly also $\hat{n}(z)$.

Scattering strength $S_v(z,f) = 10 \log [s_v(z,f)d^3]$ in decibels relative to 1(1/m^3) has the form

$$(17) \quad S_v(z,f) = 10 \log [Nd^2] + 10 \log [\hat{n}(z)d] + 10 \log [\tau(z,f)/d^2].$$

The overall level of $S_v(z,f)$ depth profiles is determined by the first term on the right-hand side of Eq. (17) containing the fish standing crop N which is geographically and seasonally dependent. The characteristic abundance term is independent of frequency and defines the basic shape of N/D profiles. This shape is uniquely modified at each ensonifying frequency f by contributions from the target strength term. In deepwater areas, particularly at low latitudes where seasonal changes are small and many bladdered species are present, our results suggest that the basic shape component of $S_v(z,f)$ depending on $\hat{n}(z)$ may be similar within different faunal provinces. The swimbladder size allometry properties of the bladdered species group are stochastic in nature (Saenger 1989) and this must be taken into account in computing the τ-contributions to $S_v(z,f)$ (Saenger 1988). The point to be made is that faunal provinces contain swimbladdered species of comparable size, and it seems probable that the size allometry properties of species groups in these provinces are very similar, if not the same, as those of the bladdered species group at OA. Physically interpreting bioacoustic data and predicting acoustic scattering properties of swimbladdered fish in the midocean is a formidable task, but it seems likely that significant advances can be made by considering the scattering contributions of bladdered species groups rather than individual species because species groups are likely to have important depth distribution and swimbladder size allometry properties in common in many ocean areas, despite differences in species composition.

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PERSPECTIVES

Taking Stock of Genetic Concepts in Fisheries Management[1]

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The historical development of the idea of isolated stocks of fish that can be managed as separate management units has been as strongly tied to the intuitive idea of separate races as it has been to the practical necessities of jurisprudence and the estimation of both biomass and sustainable yield by fisheries managers. Demonstrating the existence of isolated fish stocks and delineating their boundaries has generally proved unsuccessful. Various techniques ranging from meristic count differences to polymorphic allelism have usually failed. However, in the pursuit of isolated stocks, biochemists have uncovered a great deal of information about the variation of polymorphic allele frequencies over time and space. Following the shift in opinion away from stochastic to natural selection mechanisms in allele frequency variation, it is evident that the observed variation in allele frequencies allows more insight into the biology of fishes than into the breeding structure of populations. These insights argue against the idea of isolated stocks of fish with homogeneous growth rates that are the basis of the sustainable yield models in favour of migration-linked stocks with heterogeneous growth rates.

L'évolution au fil des ans de la notion de stocks isolés de poisson qu'on peut gérer comme s'il s'agissait d'unités de gestion distinctes a toujours été associée aussi étroitement à la notion intuitive de races distinctes qu'elle ne l'a été aux nécessités pratiques des jurisprudences et à l'estimation de la biomasse et du rendement durable par les gestionnaires des pêches. On n'est généralement pas parvenu à prouver l'existence de stocks isolés de poisson et à déterminer les limites géographiques de ces stocks. Différentes techniques utilisées, des écarts dans les dénombrements méristiques à l'allélopolymorphisme, ont habituellement conduit à un échec. Toutefois, la recherche de stocks isolés a permis aux biochimistes d'apprendre beaucoup sur la variation dans le temps et l'espace de la fréquence d'allèles à l'origine de polymorphisme. Avec le glissement de l'opinion scientifique, de mécanismes stochastiques à des mécanismes de sélection naturelle, pour expliquer les variations observées de fréquence des allèles, il est évident que les variations observées nous apprennent davantage de choses sur la biologie du poisson que sur la structure reproductive des populations. Ces connaissances vont à l'encontre de la notion de stocks isolés de poisson à taux de croissance homogènes, qui constitue le fondement des modèles de rendement durable, mais nous inclinent à penser qu'il existe des stocks à taux de croissance hétérogènes et associés à la migration.

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The biblical reference to the "birds of the air and fishes of the sea" underscores the vagility of these animals that allows them to use their medium to move great distances, often unpredictably and often with great inconvenience to man. In addition, fishes that we know to have little migratory behaviour can often change their abundance almost as abruptly as their migratory cousins. When this instability is coupled with the hardships imposed by weather, the necessity to make a profit, and the changing regulatory practices of government, it is hardly surprising that fisheries managers have always found it difficult to establish safe, sustainable yields.

In the period between the first meeting of the International Council for the Exploration of the Sea and the collapse of the North Sea herring fishery in the late 1960's, there was considerable optimism that mathematical models of the growth of fishes might allow a rationalisation of management technology. The early models of Baranov (1917) lead to the very detailed and widely used sustainable yield theories of Beverton and Holt (1957). Unfortunately, such modelling has not been a political or economic success (Anonymous 1988). One of the biological flaws in sustainable yield theory has been the necessity of some kind of equilibrium, either stationary or cyclical. Ironically, the key to understanding alternatives to equilibrium yields lies in the genetical analysis that was originally employed in the hope of demonstrating the homogeneous and isolated stocks that are essential to the concept of equilibrium yield.

In this perspective, I examine the historical development of the concept of isolated stocks and the roles of various techniques in the demonstration and delineations of such stocks. It is my contention that while those techniques have failed in their original purpose, they have presented, instead, insights into the biology of fishes that provide alternative management concepts to equilibrium yields.

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Stocks and Sustainable Yields

Fisheries managers deal with three central issues: the amount of fish caught by the fishermen's effort, the consequent economic benefits of that catch, and the policies of governments towards the activities of fishermen. The economic benefits of the catch largely determine the effort made both to catch fish and to manage the fishery and are thus of fundamental importance to any management effort. Nonetheless, the scientific, or biological, aspect of fisheries management assumes initially, at least, that the economic benefit of the catch is assured. With the assumption of profit assured, the biologists' scientific interests lie chiefly in understanding the mechanisms underlying the pattern of changes in abundance of fish populations. The biologist hopes to be able to provide quantitative data that will predict how much fish will be available to the fishermen and the consequences of various fishing regimes (the number and size of fish and the seasons of fishing) on conserving the future availability of such fishes. Biologists have generally been very successful in lobbying governments to take a conservationist approach to fisheries management. Such approaches have been of enormous value in protecting fisheries from pollution and short-sighted destruction of habitat. Firmly embedded into the conservationist approach has been the idea that the proper way to exploit fish populations is on the basis of a safe, or sustainable, yield.

In general terms, a safe or sustainable yield arises from the idea that the fisherman can take that proportion of the biomass of a fishery that is being continuously replaced by the growth of the fish. It is an idea that was advanced in Russia by Baranov (1917). It was, in its own way, a classic statement of dialectical materialism. There was a thesis (the fish), an antithesis (the fishermen), and a synthesis (the sustainable yield). Unlike the rest of the economic dialectic of the time, the sustainable yield theory has survived. Part of the reason for its survival has been because it has become embroidered with statistical theory to the point of being unrecognisable, and it is, without doubt, intellectually appealing and logically tidy as are all dialectical arguments. However, it has been as unsuccessful a paradigm for economic management as have all the other dialectical forays into economics. Nonetheless, it is firmly fixed in the minds of both biologists and politicians as the proper basis for the scientific management of fisheries.

In spite of the extensive faith shown in sustainable yield management, fisheries have almost universally collapsed in the face of sustainable yield management (Glantz 1983; Anonymous 1988). When the profitability of the fishery can no longer be assured from the yield estimates based on scientific data, other considerations (usually political and economic) become more important than biologically safe yields and the fishery manager is put into the position of organising a kind of rearguard defense of the fishery as it falls into collapse. It might be argued that the reasons for collapse are due to greed and dishonesty overcoming the prudent managers estimate of yields. There is a lot of support for that view, both from managers seeking to shift blame away from themselves and economists who see opportunities for themselves in the analysis of collapsing fish stocks. After all, economists spend a great part of their professional lives disentangling the effects of greed and dishonesty on the great theories of economics.

However, behind these problems there is still the fact that fish are real biological entities swimming around in the oceans and rivers of the world changing their abundance in time and space in response to both their environment and their fundamental genetic design. Perhaps before following Jaqueline McGlade's advice to "swap five more biologists for an economist," we should shift our biological focus from stock assessment to whatever it is that is driving the changes in stock abundance. I think that in particular, we should look at the population genetics of fish. Not for what population genetics ought to mean within the current paradigms of fisheries-oriented population or stock structure analysis, but for what population genetics can tell us about the biology of fishes. We may be pleasantly surprised. We may find that the biological processes behind the observation "... no matter how much of a mess you make, fish stocks will eventually recover if you leave them alone" (Anonymous 1988) will allow us access to a more realistic management paradigm than dialectical materialism.

Biologists have generally dealt with fishes as if all of the fish in a certain geographical area could be regarded as a single homogeneous population unit consisting of different aged, but otherwise biologically similar, fish. Biologists and fisheries managers approach the basic problems of changes in abundance as if such large homogeneous populations had some real existence. Although this view came into its present widespread usage more or less through ignorance, the persistence of the concept of separate, large, homogeneous populations of fish has been supported by a number of scientific arguments. The chief of these arguments has now come to be the genetic argument. The development of the concept of separate, large, homogeneous populations of fish (or stocks) can be followed from the point of view of the changing pressures placed on fisheries managers by economic and political, as well as scientific, considerations.

Stocks: The Change in Emphasis from Accessibility to Homogeneity

The fisheries manager describes both the availability of fish and the consequence of fishing itself in terms of "stocks." The simplest kind of "stock" would be all of the fish that are within the range of the fishing vessels under the jurisdiction of a particular fisheries manager. If the maximum range of fishing boats from a certain port is 30 miles, then all of the fish within a radius of 30 miles represent the "stock" to which the ships of that port and its fisheries managers have access.

From an economic or political point of view "stocks" simply represent the geographically defined region from within which the wealth of a fishery is drawn, and within which changes in abundance occur. Such "access stocks" can be increased in size without limitation when only economic or political interests are involved. However, in the face of practical management problems, "access stocks" acquire internal structure. Species composition is the first structural element to emerge.

In some cases the entire species may come within a fisheries manager's range and thus of itself constitute a well-defined "access stock." Many species change their geographical location over the course of their lifetime, so that fisheries managers may regard different periods in the life of a fish as constituting different "access stocks." Some fish, for example, live on shallow nursery grounds until a certain age and then move to deeper water. As a result, fisheries managers may treat "inshore" and "offshore" stocks of the same species as if they were discrete populations.

Other kinds of internal structuring of stocks arise from fisheries considerations alone. For example, Holt (1959) in a discussion of population terminology introduced the term "acces-

sible stock" to refer to the availability of certain fish to particular gear types. Following from this usage, Holt introduced the terms "vulnerable stock," "exploited stock," etc., that are essentially relative terms referring to different parts of a population that become apparent as a result of a particular fishing technique and which may, or may not, refer to the underlying biology of the fish. This view of stocks was very clearly stated by Russell (1931, p. 4):

> Let us simplify the problem down to its bare essentials by considering a completely self-contained stock of fish of one particular kind living in a large area which is systematically fished. Let us further assume that the fishing gear is standardized and is such that all the fish reaching a length L are liable to capture and that none of length less than L are caught. The total stock in the area may then be divided into those of L and upwards in length and those less than L and we shall call these respectively the catchable stock and the non-catchable stock.

It is evident from Russell's description of stocks that such stocks have a strong requirement for similarity, if not homogeneity, among the fish caught. Similarity is an important element in the internal structure of any definition of "stocks." It is particularly important to establish groups of similar animals if any kind of mathematical or statistical analysis of abundance is to be undertaken. The transformation of observations to numbers brings with it the assumption of homogeneity. One cannot sensibly compare numbers relating to apples with numbers relating to oranges unless one is aware that the numbers refer to different kinds of things. As fisheries managers turned to the direct question of measuring, and modelling, changes in apparent abundance (the pattern of fish catch rates at different times and places), so a more quantitative definition of stocks became necessary. With that quantification process came an increasing emphasis of the assumption of the homogeneity of the stock.

Stocks: The Problems of Genetic and Phenotypic Variation

Marr (1957) introduced several definitions of subpopulations of fishes in which he makes a distinction between "subpopulations" (as being both genetically homogeneous but phenotypically distinct units) and "stocks." Marr (1957, p. 1) defined "stocks" in this way:

> A stock is a population or a subpopulation all members of which are characterised by similarities which are not heritable but are induced by the environment. A stock may or may not include members of several different subpopulations.

Marr's definition of stocks is more subtle than it first appears because it recognises that the fisheries manager is interested in phenotypically similar fish — similar growth rate, fecundity, etc. — even if such fish are genetically dissimilar.

Marr (1957, p. 1) continued with a statement that should serve as a warning against too closely defining biological entities by characters that cannot be readily identified by experiment:

> The important distinction to keep in mind between subpopulation and stock is that members of a subpopulation segregate at spawning time, whereas members of a stock need not. It is also important to remember that members of a group actually are members of either a subpopulation or a stock, but cannot be assigned to one or the other category because of lack of information. The partial barriers to gene flow between subpopulations are of the same nature as those between subspecies and include isolation in space, isolation in time and ecological isolation. The 'subpopulation problem,' then, involves first, the recognition and definition of each subpopulation and second, the planning of biological observations such that the data accrue discretely for each subpopulation rather than by groups of subpopulations. If observations are planned in such a manner that data accrue discretely for each stock, little if anything will be learned about subpopulations and, in fact, if the concepts of stock and subpopulation are confused the investigator may be very seriously misled. On the other hand, the characteristics of a stock may well serve as natural tags and be of great value in the study of availability phenomena. It is a fair generality to state that whereas most fishery biologists have been interested in defining subpopulations they have, in fact, most frequently defined stocks or groups. This may be avoided only by using characteristics known to be genotypic or by using a more direct experimental method such as tagging.

While there is an underlying concern for homogeneity in Marr's approach, he appears to favour the restriction of "stock" to "access stock" in a similar usage to Holt (1959). That is, "stock" defined by nonbiological characters, or at least characters that are not heritable. Marr may have envisioned two levels of homogeneity: a superficial homogeneity of phenotype imposed by the environment onto a mixture of various genotypes, each of which remained part of a separate, and genuinely genetically homogeneous, subpopulation. One might illustrate this by regarding subpopulations that are genetically distinct as sets A, B, and C that are separate at spawning time. During the intervening periods the subpopulations might mix to form the intersection set D, which would constitute the Marr-type "stock."

From the management point of view, this is not a fruitful definition of stock because the entire species could be regarded as the stock, and subpopulations themselves would be subject to migration unless they were accorded subspecies status. However, Marr's (1957) treatment recognised that groups of fish of the same species regularly spawn at the same time, but in different places. This kind of separation of fish into subgroups is part of the common observations of every fisheries biologist and is in my opinion a major contributing factor to the insistence by many fisheries biologists that genetically homogeneous isolated groups of fish exist whether such groups can be experimentally verified or not.

The origin of this cumbersome treatment of stock no doubt lay in the difficulty of distinguishing phenotypic variation from genotypic variation. Statistical analysis of the phenotype directly had not been successful in establishing a genotypic component. While some attempts had been made by quantitative geneticists to assess the environment and genotype components of the phenotype, those techniques required breeding experiments that were not available to fisheries managers.

However, in Marr's (1957) discussion of subpopulations, he lists "blood characteristics" as a tool in separating genetic subpopulations within phenotypically similar populations. The study of these "blood characteristics" lead directly to the use of enzyme allele variation and marked a complete shift away from the idea of a phenotypically similar, but genotypically diverse, "access stock" to a genotypically similar, but phenotypically diverse, "homogeneous stock." This change of emphasis was not simply the case of a new technique introducing new insights. Marr and his colleagues had concentrated

their attention on the pelagic tuna, clupeid, and salmonid resources of the eastern Pacific. These fish typically exploit a huge area of ocean, moving from one region to another, both at different times of the year and in different years, so that one phenotypic type (e.g. vertebral number) of adult could easily produce offspring that would inhabit a different oceanic environment and so acquire a different environmentally induced phenotype. Royce (1957) and McHugh (1942) had already demonstrated phenotype plasticity in the eastern Pacific tunas and herring. Marr's distinction between the phenotypic "stock" and the genotypic "subpopulation" was quite reasonable in light of the biological problems he had encountered.

What is now commonly referred to as a "stock" or "unit stock" has its origins in the quite different situation of North Atlantic commercial species, particularly the cod and the herring. The following quotations from Gulland (1971, p. 117) will make both the similarities of management intent and the difference in stock concept between the "eastern Pacific" and 'North Atlantic' views quite plain:

> Before applying the models to the situation in a particular fishery, it is necessary to define the population, or stock of fish concerned. Ideally, a unit stock is a self-contained and self-perpetuating group, with no mixture from the outside, and within which the biological characteristics and impact of fishing are uniform. Such a unit stock would also be a genetic unit.
>
> Few groups of fish form such neat units, and the choice of what should be considered a unit stock has usually to be made empirically, in the precision and detail required in the analysis.
>
> In practice it is usually convenient to treat as large a group as possible as a unit stock, thus enlarging the amount of information available for analysis, and avoiding the need to subdivide the statistical information on catches, etc. Even when the group of fish being treated as a unit in fact contains several independent unit stocks, serious errors will not be incurred if the values of the parameters of growth, mortality, etc., do not vary between the stocks.

Gulland's "unit stock" is similar to Marr's "subpopulation": a genetically isolated unit, virtually a subspecies. However, Gulland's "unit stocks" exist as part of an ensemble of such units that constitutes the species whereas Marr's subpopulations mix out of spawning and so constitute a genetically mixed stock that is nonetheless phenotypically homogeneous. Gulland also introduced and emphasized the need for homogeneity within stocks. Clearly, homogeneous "values of the parameters of growth, mortality, etc," are essential for any kind of statistical models of abundance based on growth or mortality.

The Unit Stock and the Unit of Management

Gulland's (1971) approach raises an important point: that stocks owe their existence as much to the *need* for their existence as to the *fact* of their existence. Gulland noted that stock divisions may be made empirically and that mistakes so incurred as to the true, or underlying, stock structure will not be severe unless the differences in the properties of the stocks, such as growth rate, are so great as to make them severe. The consequences of such mistakes were examined by Ricker (1958, 1973). Ricker's contribution to the stock problem is quite critical because the amount of effort needed to establish stocks is dependent on how much damage to the future availability of fisi. will be incurred if a proposed stock structure is incorrect.

Ricker (1973) dealt with western Canadian salmon, species that have different spawning grounds that generate stocks with different growth rates that are fished when they are mixed together in the sea prior to the spawning run up the river. In these circumstances the mean growth rate of the mixture of stocks is misleading because sampling is always over a heterogeneous group. Harvesting, or allowable catch, estimates based on this mean growth rate will result in a steady loss of slow growers and will push the mean growth rate towards the fastest growers until only the fastest growing stock remains. This progress assumes that slow growers take longer to reach maturity and are therefore more likely to be caught before spawning because they are exposed to fishing pressure for a longer period.

In the case where differences in growth rate represent the different genetic constitutions that are necessary to exploit the entire range of habitats available to the species, the monoculture of fast growers resulting from fishing may mean an irretrievable decline in the total production of the species. The decline is caused not only by the loss to the fishery but also by the inability of "fast" survivors to exploit habitats formerly available only to genetically appropriate "slow" growers — decline that is irretrievable because it entails the loss of those specific genotypes adapted to the "slow" habitat. Other circumstances might arise, particularly in marine mixed fisheries, where the simultaneous removal of competitors along with the slower growing group of a population may result in a compensating effect in which there is an increase in productivity caused by fast growers exploiting niches in which they would normally be rendered suboptimal by other competing species with a more appropriate genetic design for those niches.

Nonetheless, genetic heterogeneity of growth rates and other parameters would have, as Gulland (1971) correctly implied, severe effects on fisheries yield, effects that would compromise the assumptions of the basic models of the interaction of fish and fishermen of Baranov (1917) and Beverton and Holt (1957) that assume a graded response between the productivity of the fishery and the catch rate that yields a point of equilibrium between the two. Given the time and place in which Baranov developed this basic model, it is not surprising that it is in the form of an equilibrium yield. Baranov was at the center of a dialectical ferment in Russian political and cultural life in which the idea of the fish as the thesis, the fisherman as the antithesis, and the equilibrium yield as the synthesis would have been intellectually attractive as well as politically correct.

The basic idea of stock separation, which is stock recognition in terms of genetically homogeneous units, can now be seen to be a fundamental part of fisheries management strategy, an idea that warrants very close and careful attention.

Stock Separation

Phenotype Markers

The underlying assumption that species were broken up into genetically isolated groups or races was put forward at a very early stage in the scientific management of North Atlantic fishes. For example, at the first meeting of the Conseil Permament International pour l'Exploration de la Mer the following remarks were recorded (Heincke 1902):

> It must be regarded as proved that different races of herrings, separated from one another by real distinctions, existed in the European seas, e.g. the Norwegian spring herring, the

> Scottish autumn herring, the herring of the Channel, the coast herrings of the Southern North Sea, the Baltic and others.

Heincke (1898) had based his proof of the genetical basis of different races on the so-called "Quetelets Law" which assumes that if a population is normally distributed, it must be a "pure" race, i.e. genetically homogeneous. Heincke used the normally distributed data of vertebral counts to establish races of herring. In doing so, he could rely on support from no less an authority than Karl Pearson who had used a closely parallel argument to separate races of crabs on the basis of the distribution of the proportions of carapace lengths (Pearson 1894). This was a very important paper, reflecting a fundamental attitude held by Pearson and his colleagues that the statistical properties of phenotype frequencies could be used as a reliable guide to understanding the biology, particularly genetics, of organisms. Others thought differently, leading to an unhappy division between "biologists" and "statisticians" that is, in population genetics at least, with us to this day (Provine 1971).

Although Pearson's (1894) view can be disputed on the grounds that the normal distribution could not provide a suitable test of homogeneity, it was Schmidt (1917, 1923) who undid most of this separation into genetically distinct races based on vertebral number by demonstrating that the temporal variation in vertebral number was induced by the environment. Later attempts to establish races, or unit stocks, of fish with other techniques have encountered exactly the same problem, so that Schmidt's (1923, p. 19) comments are worth repeating at length:

> With investigations as to local races of fishes and other organisms, it must from the nature of the case be of great importance to ascertain whether the average values taken as characterising the races (the "racial characters") remain constant in the same populations from year to year. For it is obvious that all conclusions regarding the difference between two populations in respect of origin must be highly conditional, if it should be found that the qualities by which the populations are distinguished themselves fluctuate greatly from year to year. Generally, however, too little attention has been devoted to this important question. Investigations have as a rule been restricted to the comparison, without further analysis of populations from two or more waters and the attempt to decide — by mathematical means — whether any difference could be discerned between the populations concerned.

Schmidt did not argue that races of herring did not exist, only that vertebral number did not provide a suitable tool for establishing such races. The appropriate tool would have to be one that was not affected by changes in the environment, or the idea of local, genetically isolated races would have to be abandoned in favour of a much larger genetic unit. However, other observers of cod and herring in the North Sea strongly favoured local races.

Russell (1931, p. 9) said in reference to the cod:

> The life-history and migrations of a fish-group. . .take place within a closed circle: as a rule the fish move up-stream to spawn and their eggs and larvae are distributed down-stream by the currents: spawning areas and feeding areas are often distinct and may be widely separated, and migrations are mainly for the two purposes of feeding and spawning.

Russell referred to earlier work on cod by Damas (1909) to support this "fish-group" concept.

Hodgson (1934, p. 48) presented much the same picture for herring:

> ...spawning migration is against the stream, or contra-natant as it has been called. Thus the herring, in common with many other fish carries out the obvious movement in going upstream to spawn so that under normal conditions its young will be brought back to the same area whence the parents came.

In addition, many countries exploited the fish resources of the North Sea, often on the basis of traditional fishing grounds, so that there were also considerable political advantages to having the North Sea fish resource neatly packaged into local races. The same political pressures did not exist in the eastern Pacific.

Vertebral number, fin ray number, and other phenotypic characters have continued to be used by some workers as at least partial markers for races (Casselman et al. 1981). More cautious views of such phenotypic variation are often expressed by taxonomists who have continued to study the variation in phenotype characters as a topic of research in its own right (Lindsey 1981).

Red Blood Cell Antigen Frequency Markers

In the early 1930's, red blood cell antigen frequencies were investigated as a possible tool for separating genetically isolated races (de Ligny 1969). Red blood cells have surface antigens and the blood plasma contains the complementary immune antibodies in solution. These two components give rise to the well-known "blood type" effect. Just as human populations have different, and often characteristic, "blood type" frequencies, so do other vertebrates, including many fish species. Different red blood cell antigens are regarded as allelic variants of one or more loci; consequently, red blood cell antigen frequencies can provide the basis for analysis of the genetical structure of populations.

Red blood cell antigens and their appropriate antibodies had obvious physiological differences that were readily demonstrated by inappropriate transfusions in humans. But their adaptive value was considered by many to be nil. Stormont (1961), for example, could make the following statement:

> ...it is axiomatic in immunogenetics that all blood factors are inherited traits which are subject to little or no influence by the environment. Consequently, any differences which two or more subpopulations may exhibit with respect to the incidence of common blood factors are fully meaningful even in the absence of information concerning the inheritance of blood factors...

This was not an unusual attitude amongst many biologists in regard to many characters, especially amongst taxonomists; for example, Robson and Richards (1936, p. 19) said the following:

> A survey of the characters which differentiate species (to a less extent genera) reveals that in the vast majority of cases the specific characteristics have no known adaptive significance.

Other geneticists believed that blood group genetic variation had considerable adaptive significance, and generally their point of view has been substantiated. Nonetheless, a very large number of studies were conducted (see review by de Ligny 1969) aimed at stock separation.

The use of red blood cell antigen and antibody frequencies to define stocks fell into disuse, but not for the obvious reason

that they were adaptive features of blood cells. The main reason was that the proteins involved proved to be systematically altered by various posttranslational modifications. A wide number of "factors," small and large polypeptides, are involved in the immune response so that observed red blood cell antigen frequencies would very often depend on the physical state and disease history of the fish (Hougie 1972). There are also some experimental difficulties encountered when otherwise accessible red blood cell surface antigens are "coated' with certain plasma proteins, making it necessary to undertake a variety of cleaning and other preparatory steps. Other red blood cell antigen/antibody studies in fish had already shown very complicated patterns of occurrence that would require lengthy breeding and biochemical analyses to resolve (Altukhov et al. 1969).

Protein Allele Markers

A further reason to discard antigenic methods was the appearance of electrophoresis in the mid-1960's. Electrophoresis of protein allelic variants indicated a system of a few codominant alleles with a readily interpretable genetic basis (allelic variants are the proteins coded for by the different alleles occurring at a polymorphic locus).

At about the same time as the development of electrophoresis as a tool for separating protein allele variants, Kimura (1960) put forward the first paper that would eventually lead to the Neutral Theory of Allelic Variation (Kimura and Ohta 1971; Lewontin 1974). This theory maintains that most electrophoretically detectable allelic variation results from differences in the charge state of the protein that do not affect the adaptive value of the protein. Thus, the observed differences in gene frequency inferred from the protein transcribed from those genes must be due to genetic drift, not selection. Genetic drift is the sum of various stochastic processes related to population size, breeding behaviour, and degree of genetic isolation. The neutralist view was espoused by many fisheries geneticists (Jamieson 1974; Allendorf and Utter 1980). Protein allelic variants rapidly replaced red blood cell antigens and antibodies as genetic markers that could be considered free of any environmental influence. Provided that it could be shown that no selection had taken place, then any statistically significant differences in allele frequency between two populations could only mean that they were not interbreeding. In this way, "stocks" of the traditional North Atlantic type, genetically isolated races, the Gulland stock type, could be detected. The "genetic unit stock" thus became the most common view of what a "stock" is, and the "stock" type defined by Marr (1957) fell into disuse.

The genetic unit stock had now acquired a significant role in fisheries management strategy. Not only did it provide a means of breaking the fishery into manageable units, but it also implied that there was free interbreeding within such stocks that were therefore genetically homogeneous. Traits, such as growth rate, were then, by implication, reliably measured by the population average. This is an important point. Genetic homogeneity implies that the mean and variance of biological parameters are true underlying properties of the population itself, not parameters unique to a particular sample. The mean growth rate of a population becomes a better predictor of the growth rate of new recruits than the growth rate of the parents of those recruits. The application of mean values and variances in any mathematical model assumes that such values reflect underlying properties of the population concerned. Otherwise, such models would be entirely without predictive or explanatory value. The problem of genetic heterogeneity raised by Ricker (1973) does not arise with such stocks. Cushing (1982) has been one of the strongest proponents of genetic unit stocks and provided a detailed description of such stocks. Although many fisheries biologists have accepted the genetic unit stock concept, it contains some serious deficiencies.

Cushing (1982, p. 49) described the unit stock in this way:

> ...often has a fixed spawning ground, single short spawning season, probably a consistent migratory circuit. An ideal unit of population is one in which the chances of mating are randomly distributed. Ideally, spawners do not leave the stock or join it from year to year: we cannot establish this point directly, but the genetic evidence to be given below suggests that it is true.

The crucial point of this stock definition is that "spawners do not leave ... or join." It is this that makes the stock genetically isolated; all the rest above follows. Cushing noted that isolation cannot be proved directly, so that the entire weight of the unit stock argument falls back onto the genetic evidence. Apart from the genetic isolation argument, Cushing's stock definition is not really very different from the "fish-group" concept advanced by Damas (1909), Russell (1932), Hodgson (1934), and no doubt even earlier workers in this field.

Cushing (1982) used a number of species as examples of his unit stock. For the Arctic cod the nongenetic evidence for a unit stock was based on correlation between year classes (which can arise from a number of ways not necessarily related to stock structure): minor differences in otolith morphology, vertebral sum, and fin ray count (all of which are subject to environmental variation) and the assertion that "evidence of single or unit stock is that the hydrographic mechanism exists" (Cushing 1982, p. 50).

For the North Sea herring the main argument for different unit stocks was differences in growth rate. One might feel uneasy about using differences in growth rate to define stocks when one is establishing stocks in order to establish the validity of differences in population growth rates (amongst other important traits). In addition, Cushing (1982) persisted in using vertebral count as a racial marker in herring in spite of its unfortunate history.

Cushing (1982), quoting Thompson and Herrington (1930), argued that tagging has demonstrated stock isolation in Pacific halibut. A more recent review of the Pacific halibut stock problem (Skud 1977) based on all the available sources of information concluded the following:

> ...the biological evidence clearly shows that the movements and range of halibut stocks overlap during all life stages...this interrelationship necessitates that the stocks be managed as a unit or in close coordination.

Generally, tagging studies are not a reliable guide to genetic mixing. Larval drift, for example, can result in gene flow. The numbers of tagged fish are usually quite small compared with the total population size, and only a few emigrants (1 in 50 000 per generation) would be required to maintain genic similarity between two populations (Maruyama 1971).

Nongenetic evidence for "unit stocks" is weak, even though the idea of "unit stocks" has tremendous intuitive appeal. The real argument for "unit stocks" lies in the use of genetic information. Cushing (1982, p. 49) introduced the genetic argument for stock separation in the following way.

> Some differences of biochemical origin are genetically determined. If stocks were distinct, isolated and coherent from generation to generation, one would expect genetic differences to arise, some of which could be detected by biochemical means.

The "genetic differences" are differences in proportions of alleles (usually enzyme alleles) and statistical methods are used to test whether there is a significant difference between samples.

The method outlined by Cushing (1982) tests whether populations have been subject to random, selection-free segregation by the Hardy–Weinberg law, and following that, uses single (e.g. chi-square test) or multivariate (genetic distance) statistics to test whether or not there are statistically significant differences in allele proportions between stocks. This procedure is more or less that followed by biochemical geneticists working on the fish stock problem (Jamieson 1974; Allendorf and Utter 1980).

Weakness in the Genetic Argument: The Biology of Protein Alleles

Unfortunately the genetical method supported by Cushing (1982) conceals several severe problems. The Hardy–Weinberg law is for various reasons unsuitable for testing either random segregation, selection, or stock mixing. Allele frequencies when measured over time as either replicate samples, or as different year classes, often show considerable variation (Gauldie 1984). Thus the temporal variation in allele frequencies within stocks is often as great as geographical variation in allele frequencies between stocks. The significance and analysis of temporal and geographic variation in allele frequency depend to a large extent on the underlying assumptions of either selection or genetic drift as the cause of variation. Genetic drift and sampling errors can be modelled on the basis of frequency data because of their stochastic behaviour (Waples 1989), but selection requires information about the changes in the underlying causes of selection before modelling is possible.

A much deeper, and far more serious, difficulty is raised by the neutral theory that the biochemical differences between alleles that permit electrophoretic separation are not sufficiently important physiologically to give rise to differences in fitness between individuals with alleles. Many biochemical geneticists either believe in the neutral theory of allelic variation or organise their experimentation and analysis in such a way that the neutral theory is implicit in their results. Accumulated evidence has for some time strongly indicated that there are physiological differences between alleles that are likely to lead to adaptive differences between geneotypes in regard to traits like growth, fecundity, disease resistance, etc. (Gauldie 1984; Mork et al. 1984; Nevo et al. 1984). Therefore, the variation in allele frequency that has been observed amounts to genetically programmed physiological heterogeneity in those traits. It is a cruel irony that the different alleles, whose proportions were used statistically to define genetically isolated homogeneous populations, should be, by their very existence, direct evidence of the genetic heterogeneity that makes genetically isolated homogeneous populations unlikely.

A further difficulty arises when one considers how many amino acid replacements, and of what kind, are possible in, say, haemoglobin, and still retain the haemoglobin function. Even though the structures of some haemoglobins are well known both in their conformation and their amino acid sequences, it is difficult to judge how many amino acid sites could be changed before the haemoglobin function is lost. However, there are about 20 amino acid differences between human haemoglobin and myoglobin, a related oxygen-carrying protein. One might, therefore, reasonably consider that up to a maximum of 20 amino acid sites could be changed before a change occurred in the haemoglobin function. Allowing between two and three different kinds of amino acid substitution possible at each site, there would be between 400 and 8000 different haemoglobins possible. There are certainly more than 200 000 species of vertebrates and invertebrates that use haemoglobin, which implies an enormous amount of convergence in haemoglobin polymorphism. Similar arguments can be made for enzymatic proteins that have a high requirement for a particular conformation. Even structural proteins show an extraordinary similarity in amino acid sequences, e.g. between the different collagen-like as well as between the different keratin-like proteins from different species, similarity that implies a sharp selection-driven convergence in polymorphisms for structural proteins. Convergence driven by selection for different physiologies negates any kind of statistical argument based on the assumption of random processes for either genetic isolation or time-dependent genetical divergence. The explanation for changes, or differences, in allele proportions must be sought in the physiology of the protein coded by the allele, not in the biologically sterile mean and variance statistics of allele proportions.

It is evident that the switch from a vertebral, or meristic, kind of phenotype to a "genetical" kind of phenotype has resulted in little progress in understanding stocks since Schmidt (1917, 1923). I believe it is because we have, as fisheries managers, asked the wrong questions. Suppose that Heincke (1902) had not introduced the question of race at all, but rephrased his remarks in the following way

> It must be regarded as proved that groups of herring consistently appear at certain times and places in the European seas, e.g. the Norwegian spring herring, the Scottish autumn herring, ... etc.

From this starting point, groups instead of races, the Marr-type of stock is a natural development from which, in turn, arises questions of how much effect fishing in one time and place has on the fish that appear at other times in other places, not whether fish from different areas interbreed. Such questions are independent of any question of genetic similarity or dissimilarity and can be answered from a combination of tagging experiments (Gauldie 1988) and catch statistics.

The process of divorcing genetics from biology reaches its nadir in the use of mitochondrial DNA in stock separation studies. The use of mitochondrial DNA requires the splitting of the DNA of the mitochondrion into a variety of different-sized sequences of codons by site-specific enzymes. All of these different-sized pieces are then effectively seived into like-sized groups along a separation gradient. Staining, or direct measurement of the amount of DNA in each like-sized group, is then used to give what is, in effect, a frequency polygon of the number of pieces in each like-sized category that ranges from small numbers of codons to larger numbers of codons. Statistical analyses are then used to assess the differences between frequency polygons in what are more or less familiar simple (chi-square) and complex (genetic distance) stock separation statistical models. There are a number of problems with the use of mitochondrial DNA.

The only possible rationale for using bits of DNA is that the order of codons is less significant than the juxtaposition of codons. This seems to be an unlikely prospect. Mitochondria operate under extremely tight physiological constraints (Atkinson 1977) that imply stringent selection on their proteins and hence the DNA that codes for those proteins. Many of the enzymes associated with the citric acid cycle of the mitochondrial compartment are polymorphic and their polymorphism is thought to be maintained by selection (Nevo et al. 1984). There are, in fact, major metabolic adaptations associated with the phylogenetic distribution of glycolytic and gluconeogenic pathways in invertebrates (Saz 1971). Insects and fishes that are likely to have a glycolytic α-ketoglutarate decarboxylation coupled to oxaloacetate reduction as an alternative mitochondrial pathway for intermediary metabolism under anoxic condition and a gluconeogenic glycerophosphate cycle, which is a shuttle system in which NAD-linked substrates enter and leave the mitochondria (Sacktor 1971).

Even if the DNA variation of mitochondria was not under selective constraints, and if the neutrality assumptions necessary for the mitochondrial DNA analyses were correct, there are still major problems. Mitochondria are inherited from the mother in the cytoplasm of the egg and multiply by simple division. Mitochondria are therefore haploid. It has been shown by Feller (1968, p. 379) that haploid and diploid populations can be expected to have quite different trajectories towards fixation. Haploid populations will come to fixation more rapidly than diploid populations, as has been demonstrated experimentally in multinucleated protozoa that provide an experimental analogue for mitochondria (Schensted 1958). Therefore the information that might be contained in the mitochondrial genome cannot be used to assess the significance of time-dependent variation of the somatic genome and is therefore of little value in any biological context outside of the mitochondrion itself. Even within the context of the mitochondrion there are severe problems. Mitochondrial DNA is not protected by proteins in the same way as nuclear DNA. Consequently, mutations are accumulated over the life of individuals, as well as over the life of the species (Bunn and White 1985). It has been hypothesised that in humans the accumulation of mitochondrial mutations over an individual's life is an important contributor both to the process of ageing and to several human degenerative diseases (Linnane et al. 1989), an hypothesis that is apparently supported by the data of Trounce et al. (1989). Unfortunately, studies of fish mitochondrial DNA do not give enough data to identify age, but it is evident from the literature that species that are known to have high longevity also have high levels of mitochondrial DNA mutations, e.g. sturgeons (Brown et al. 1988), while species with low longevity also have low levels of mitochondrial DNA variation, e.g. albacore tuna (Graves and Dizon 1989). Further research will be necessary to determine the age dependency of mitochondrial DNA before its role in any kind of population analysis can be decided.

There are strong parallels between the tacitly neutralist approach to population genetics theory and the tacitly equilibrium yield approach that is still widely practiced in fisheries management. Both approaches assume that intrinsic data, such as allele frequency and size frequency, contain all the information required to predict the future state of the system. In practice, this assumption requires that the sample mean and variance are good estimates of the population mean and variance. It is this parallelism that has lead the inevitable application of the stationary gene frequency concept to what is statistically the very similar equilibrium yield concept. The selectionist view is that sample mean and variance are very poor estimates of the population mean and variance because, by definition, the population is (except in rare circumstances) in a state of change from one species configuration to another species configuration which includes allelic variation, size frequency, meristic character, and abundance.

I think that I have presented enough evidence in this paper to show that the parallelism between neutral allele theory and the stock concept central to equilibrium yield theory has not been useful in fisheries management. We must now consider allelic variation in terms of the biological implications of the observed patterns of allelic variation.

Environmental Dynamics

Although population genetics data may be superfluous to the issues of fisheries management of stocks, they draw attention to the dynamics of the interaction between fishes and their environment. Both the plasticity of meristic phenotypes (such as vertebral count) and the occurrence of different polymorphic proteins in different environments show that fishes stretch their physiological resources to the limit in the competition for survival. This kind of situation does not bode well for fisheries management. Most fisheries management models — and all equilibrium yield models — assume that fish will continue to grow and reproduce at least at the same rate (and perhaps increased rates) while fishing occurs in order that some equilibrium between catch and fish production may be struck. If fish are genetically heterogeneous, with differences in growth rate and reproductive capacity over space and time, then convergence to an equilibrium between growth rate and catch rate will be unlikely and will occur only transiently, if at all. If we add the strong likelihood that such heterogeneity is already stretched to the limit by stringent selection from competitors and environment, then it becomes very unlikely that any equilibria between fishing pressure and abundance will exist. And that, unfortunately, is consistent with the history of fisheries management. With rare exceptions, significant fishing effort occurs in parallel with a decline in abundance well below calculated "safe" equilibrium yields, often with unprofitable consequences for commercial organizations that have invested in the long-term expectation of profitability implied by the equilibrium yield theory.

An alternative approach would be to regard fish populations as being inherently unstable, capable of fluctuating from high to low levels of abundance, in fact "designed" by natural selection to do exactly that. The very existence of protein polymorphisms bespeaks a history of fluctuating numbers because selection by the environment can only occur by significant change in mortalities. Our fisheries management policies would be in much closer harmony with nature if we introduced policies of deliberately cycling fishing effort over periods compatible with natural cycles of abundance, rather than cycled fishing effort over periods related to the economic history of the fishery. However, this is not a politically sustainable option. There are numerous examples of fisheries that have been deliberately overfished for economic reasons even when good-quality biological data were available to show that overfishing was occurring (Radovich 1987; Fraidenberg and Lincoln 1985). To some extent this kind of overfishing problem might be overcome by using adaptive as well as prescriptive management strategies that include life histories (Rothschild and Heimbach 1983). The

adaptive aspect of fisheries management strategy might be stretched to include deliberate overfishing if it were known what the long-term risks of overfishing to fish abundance really are. It is in this area of risk assessment that population genetics may yet have its most important role to play in fisheries management.

We know that abundance of fishes is affected by nature as well as by man. Indeed, natural changes in abundance are the basis for all adaptive management strategies. Even fish species that are under heavy pressure from the fishery show large changes in abundance that are essentially independent of the fishery (Kawai and Isibasi 1983). Very little effort has been spent on assessing the effects of the biochemical and physiological variability implied in genetic polymorphisms on the relation between low levels of abundance and the capacity for accelerated rates of recruitment to high levels of abundance when the population is released from fishing pressure. This potential resilience should be included in fisheries management strategies in situations in which there may be valid economic reasons for going past conventional biological limitations on catch and effort. The hypothesis that mitochondrial DNA variation may be accumulated over the life of individuals is particularly apposite to the question of genetical risk assessment. Many protein polymorphisms occur in mitochondrial enzymes, and having a potential marker of individual fitness in the accumulation of mitochondrial DNA mutants to compare with at-spawning genetic variation of individuals should provide a unique window into the complex problem of assessing the importance of genetic variability in the resilience of populations with severely truncated age distributions.

However, this approach also means a reassessment of our conventional ideas of what is meant by living in harmony with nature. Living in harmony with nature has become a major political issue with the growing worldwide success of ecology-oriented "green" politics. Equilibrium yield has been widely identified with the concept of living in harmony with nature and is regarded by many as the only acceptable course in the wise utilization of fish resources. This is due partly to the simplicity of the idea itself and ignorance of the realities of natural fluctuations in abundance. Living in harmony with nature means that we must accommodate her jagged chords and abrupt pianissimi, an accommodation that may be of great value in matching politics and economics to abundance, but an accommodation that requires a much better understanding of the biological role of genetic variation than we presently have.

If we persist in ignoring the biological information in protein polymorphisms in favour of the assumption of stationarity implicit in statistical analyses of gene frequencies, we run the risk of further expensive and biologically sterile investigation into nonexistent genetically isolated "stocks" while fisheries continue to collapse and legitimate fishing enterprises are bankrupted.

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Volume 48, No. 4, April 1991

Volume 48, nº 4, avril 1991

Welch, D. W., and D. J. Noakes. Optimal harvest rate policies for rebuilding the Adams River sockeye salmon (*Oncorhynchus nerka*) **526–535**

Bergman, E. Changes in abundance of two percids, *Perca fluviatilis* and *Gymnocephalus cernuus*, along a productivity gradient: relations to feeding strategies and competitive abilities **536–545**

Appelberg, M., and E. Degerman. Development and stability of fish assemblages after lime treatment **546–554**

Bradford, M. J. Effects of ageing errors on recruitment time series estimated from sequential population analysis **555–558**

Kuris, A. M., S. F. Blau, A. J. Paul, J. D. Shields, and D. E. Wickham. Infestation by brood symbionts and their impact on egg mortality of the red king crab, *Paralithodes camtschatica*, in Alaska: geographic and temporal variation **559–568**

Bowen, S. H., D. J. D'Angelo, S. H. Arnold, M. J. Keniry, and R. J. Albrecht. Density-dependent maturation, growth, and female dominance in Lake Superior lake herring (*Coregonus artedii*) **569–576**

Birt, T. P., J. M. Green, and W. S. Davidson. Mitochondrial DNA variation reveals genetically distinct sympatric populations of anadromous and nonanadromous Atlantic salmon, *Salmo salar* **577–582**

Webb, P. W. Composition and mechanics of routine swimming of rainbow trout, *Oncorhynchus mykiss* **583–590**

Fournier, D. A., J. R. Sibert, and M. Terceiro. Analysis of length frequency samples with relative abundance data for the Gulf of Maine northern shrimp (*Pandalus borealis*) by the MULTIFAN method **591–598**

Jones, M. L., C. K. Minns, D. R. Marmorek, and K. J. Heltcher. Assessing the potential extent of damage to inland lakes in eastern Canada due to acidic deposition. IV. Uncertainty analysis of a regional model **599–606**

Parrish, D. L., and F. J. Margraf. Prey selectivity by age 0 white perch (*Morone americana*) and yellow perch (*Perca flavescens*) in laboratory experiments **607–610**

Singer, T. D., and J. S. Ballantyne. Metabolic organization of a primitive fish, the bowfin (*Amia calva*) **611–618**

Bajdik, C. D., and D. C. Schneider. Models of the fish yield from lakes: does the random component matter? **619–622**

Hsieh, W. W., W. G. Lee, and L. A. Mysak. Using a numerical model of the northeast Pacific Ocean to study the interannual variability of the Fraser River sockeye salmon (*Oncorhynchus nerka*) **623–630**

Testa, J. W., G. Oehlert, D. G. Ainley, J. L. Bengtson, D. B. Siniff, R. M. Laws, and D. Rounsevell. Temporal variability in Antarctic marine ecosystems: periodic fluctuations in the phocid seals **631–639**

Rubec, P. J., J. M. McGlade, B. L. Trottier, and A. Ferron. Evaluation of methods for separation of Gulf of St. Lawrence beaked redfishes, *Sebastes fasciatus* and *S. mentella*: malate dehydrogenase mobility patterns compared with extrinsic gasbladder muscle passages and anal fin ray counts **640–660**

Tallman, R. F., and M. C. Healey. Phenotypic differentiation in seasonal ecotypes of chum salmon, *Oncorhynchus keta* **661–671**

Johnson, T. B., and D. O. Evans. Behaviour, energetics, and associated mortality of young-of-the-year white perch (*Morone americana*) and yellow perch (*Perca flavescens*) under simulated winter conditions **672–680**

Rakocinski, C. Prey-size relationships and feeding tactics of primitive stream-dwelling darters **681–693**

Brooks, A. L., and R. A. Saenger. Vertical size–depth distribution properties of midwater fish off Bermuda, with comparative reviews for other open ocean areas **694–721**

Perspectives

Gauldie, R. W. Taking stock of genetic concepts in fisheries management **722–731**

Announcements/Avis **732**

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